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HYDROPTILIDAE (TRICHOPTERA) OF COSTA RICA AND THE NEOTROPICS: SYSTEMATICS OF THE GENUS *BYRSOPTERYX* FLINT (STACTOBIINI)

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Abstract.—The systematics of the genus *Byrsopteryx* are reviewed. Two previously described species, *B. mirifica* Flint from Venezuela, the type species of the genus, and *B. septempunctata* (Flint) from Dominica are redescribed and illustrated. In addition, 11 new species are described and illustrated: *B. chaconi, B. cuchilla, B. esparta, B. gomezi, B. solisi, B. tapanti,* and *B. tica* from Costa Rica; *B. loja* and *B. rayada* from Ecuador; and *B. abrelata* and *B. espinhosa* from Brazil. Keys to species for males and females are presented. The genus is transferred from the Leucotrichiini to the Stactobiini. A species level phylogenetic analysis reveals that the Costa Rican species form a monophyletic group.

Seven undescribed species of the microcaddisfly genus *Byrsopteryx* Flint were collected recently in Costa Rica by R. W. Holzenthal and his colleagues, during a survey of the country's Trichoptera fauna. This inventory, sponsored by the National Science Foundation, and coordinated through the Costa Rican National Biodiversity Institute, has thus far recorded 445 caddisfly species from the country. The family Hydroptilidae, or microcaddisflies, represents 31% of the known fauna's species diversity, and 56% of the Costa Rican microcaddisflies are undescribed.

Additional *Byrsopteryx* specimens from Ecuador and Brazil (with two new species each) were obtained from the National Museum of Natural History, Smithsonian Institution, made available through the collecting efforts of Dr. Oliver S. Flint, Jr. Examination of the Costa Rican and South American material prompted us to review the genus in its entirety and to prepare this, the third in a series of papers on the Hydroptilidae of Costa Rica and the Neotropics.

The genus was established by Flint (1981) for the Venezuelan species *Byrsopteryx mirifica.* In the same paper, *Alisiotrichia septempunctata* Flint, 1968, from Dominica was transferred to *Byrsopteryx.* We redescribe these two species in the present paper. Earlier, we described the larva of *B. mirifica* and discussed the phylogenetic placement of the genus within the Leucotrichiini (Holzenthal and Harris, 1992). We suggested then that *Byrsopteryx* more properly belonged in the Stactobiini. This opinion has been expressed elsewhere (Flint, 1992; Harris and Flint, 1993; Harris and Holzenthal, 1993) and we here formally transfer *Byrsopteryx* to the Stactobiini. Finally, in the present paper, we discuss the phylogenetic relationships of the species of *Byrsopteryx* and present a key to males and females.

Types of species described in this paper, as indicated in the text, are deposited in the collections of the National Museum of Natural History, Smithsonian Institution,

Washington, D.C. (NMNH), the University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP), the Instituto Nacional de Biodiversidad, Santo Domingo, Heredia, Costa Rica (INBIO), and the Museu de Zoologia, Universidade de São Paulo, Brazil (MZSP) [note: types in the MZSP are on indefinite loan to the NMNH, O. S. Flint, Jr., pers. comm.]. All type material is pinned, unless noted otherwise. In Figures 8–20 of male genitalia, A, B, and C are lateral, dorsal, and ventral views, respectively, of abdominal segments VIII–X; D and E are lateral and ventral views, respectively, of the phallic apparatus. In Figures 21–30 of female genitalia, A is a ventral view of abdominal segments VI–XI, and B is an enlarged, ventral view of the vaginal apparatus.

Byrsopteryx Flint

Byrsopteryx Flint, 1981:27. Type species: *Byrsopteryx mirifica,* by original designation.

Diagnosis: Adults: Small, total length 2–3 mm. Easily recognized by prominent white or greenish-white spots (elongated into stripes in one species) on dark fuscous body and forewings (Figs. 3, 4, 6, 7). *Coloration:* Frons covered with white setae; antennae of some species covered with white setae, otherwise fuscous; mesoscutum laterally with large, oval patches of white setae, often coalescing medially; in some species the legs, especially forelegs, with white setae along anterior edges; forewing with elongate spot at base of medial area, an oval spot along the midcostal border, an oval subapical spot, and in some species a small spot at the apex of the wing. No sexual dimorphism in color. Central area of forewing thickened with distinct "line of weakness" (Flint, 1981) separating a posterobasal area (Fig. 5C); large retinaculum of thick white setae present on under surface of forewing at midlength of somewhat thickened costa, apparently used to couple wings (Fig. 5C inset). Hind wing with patch of hooked setae (frenulum) near midcostal border (Fig. 5C) which engages forewing retinaculum. Venation reduced in both wings. Antennae simple with 17–19 segments. Ocelli three. Mesoscutum with transverse suture, metascutellum subpentagonal (Fig. 5A). Tibial spur formula 0, 3, 4 (Fig. 5B).

Male genitalia: Complex, structures often difficult to discern and homologize among the species and related genera. Segment VII without ventromesal process. Segment VIII quadrate, tergum shorter than sternum; long, stout setae usually present ventrolaterally, VIII often with dorsolateral processes (especially Costa Rican species). Segment IX recessed within VIII, with distinct dorsolateral appendagelike processes in most species, which may be bifid. Segment X typically reduced to membranous lobe with only lateral portions sclerotized, but in some species apicoventral portion developed into sclerotized, lyre-shaped process. Inferior appendages typically fused into ventral tubular structure, but absent in some species. Subgenital plate present or absent. Phallic apparatus complex, with wide basal section and cylindrical distal portion often bearing spines or sclerotized processes, middle region of phallic apparatus usually very constricted.

Female genitalia: Segment VI with short ventromesal process in two species, absent in others. Segment VII elongate, sternum often slightly emarginate posteriorly. Segment VIII with pair of elongate lateral apodemes and ring of stout setae posteriorly. Segment IX short, bearing pair of elongate lateral apodemes. Segment X + XI short,


1


2


3


4

with pair of thin papillae apically. Vaginal apparatus (incorrectly referred to as "bursa copulatrix" by Holzenthal and Harris [1992]) variable among species, but usually with elongate tubular process associated with posterior half and mesal sclerotization.

Larvae: Known only for *B. mirifica* (Holzenthal and Harris, 1992) and *B. chaconi,* n. sp. Abdomen laterally compressed, thoracic nota and abdominal tergites heavily sclerotized, especially on abdominal segments VIII and IX. Pronotum anterolaterally with paired depressed areas and pair of short, stout setae. Case purse-like and constructed of silk.

Biology: Larvae are madicolous and crawl, within their portable cases, in the spray and splash zones of small waterfalls and on boulders in small streams (Figs. 1, 2). They probably feed by scraping diatoms and other periphyton from the substrate. Aggregations of pupae are found above the waterline in pits and depressions on the sides of wet bedrock and boulders.

The strikingly colored adults very actively run for short distances, changing direction quickly, over streambed rocks, boulders, and large leaves of low riparian vegetation. Occasionally they quickly stop and freeze in position. When disturbed they deftly fly off to another area. Their contrasting black and white coloration and enlivened movements almost mimic the activity of certain ants. Adults are most active in the bright sunlight at any time of day. They only rarely fly to collecting lights at night and are best collected with an aspirator as they run about on the ground.

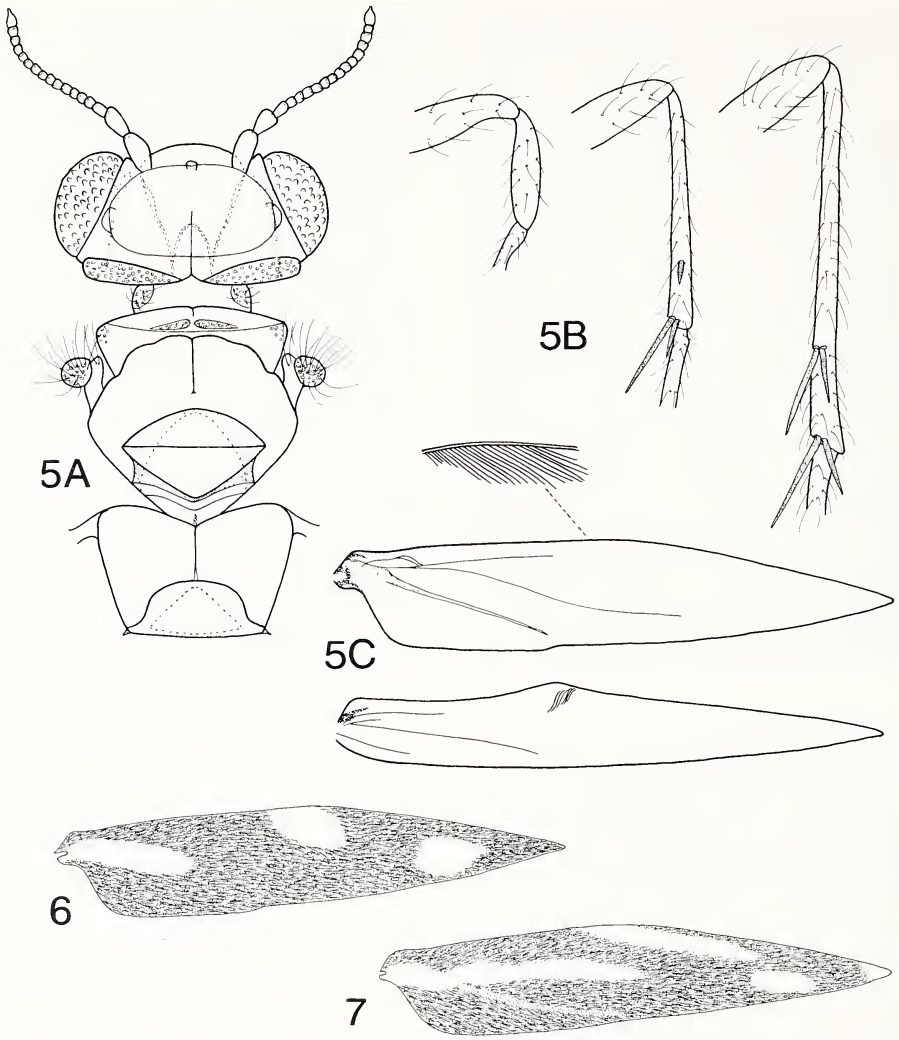
Byrsopteryx abrelata, new species
Figs. 8, 25

The incised posterolateral margin of segment IX of the male and the acutely pointed dorsolateral process of this segment distinguish the species. The circular sclerite of the female vaginal apparatus is distinctive.

Male: Length 3.2–3.3 mm. Antennae with 17 segments. Forewing coloration as in Figure 3, except spots somewhat smaller, rounder, with additional, small patch of white setae at middle of anal border. Legs with white setae. Genitalia as in Figure 8. Segment VIII with tergum shorter than sternum; posterior margin broadly rounded and extended ventrolaterally, emarginate ventrally and bearing short setae. Segment IX recessed within VIII, narrowing anterodorsally in lateral view, deep mesal incision anteriorly in dorsal and ventral views; posteriorly with lateral margin incised and with elongate dorsolateral process, narrowing distally, downturned apically to acute point; in dorsal view lateral process narrow, turned mesally, posterior margin incised. Inferior appendages absent. Segment X narrow, largely membranous, without setae; sclerotized laterally. Subgenital plate in ventral view, wide basally, rounded apically with mesal projection; in lateral view, truncate, with pair of acute, apical points.

←

Figs. 1–4. 1, 2. Habitats: 1. Type locality of *Byrsopteryx chaconi,* n. sp., roadside waterfall and seeps of Río Grande de Terraba, along Panamerican Highway, Puntarenas Province, southeastern Costa Rica. 2. Type locality of *Byrsopteryx tapanti,* n. sp., waterfall on Quebrada Palmitos, Tapantí National Wildlife Reserve, Cartago Province, central Costa Rica. 3, 4. *Byrsopteryx* spp., habitus. 3. *B. gomezi,* n. sp. 4. *B. rayada,* n. sp.



Figs. 5–7. *Byrsopteryx* spp. 5. *Byrsopteryx mirifica* Flint: A, head and thorax, dorsal; B, fore, middle and hind tibiae; C, fore and hind wings; inset, retinaculum. 6. *B. chaconi,* n. sp., forewing coloration. 7. *B. rayada,* n. sp., forewing coloration.

Phallic apparatus somewhat simple, wide basally and apically, with narrow, elongate, apically bifid, central spine, in lateral view spine upturned.

Female: Length 3.2–3.5 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 25. Segment VII elongate, sternum with slightly emarginate posterior margin. Segment VIII short and wide, posterior margin slightly emarginate with ring of stout setae; laterally with pair of elongate apodemes extending to posterior of segment VI. Segment IX short, narrow, with lateral apodemes extending to middle

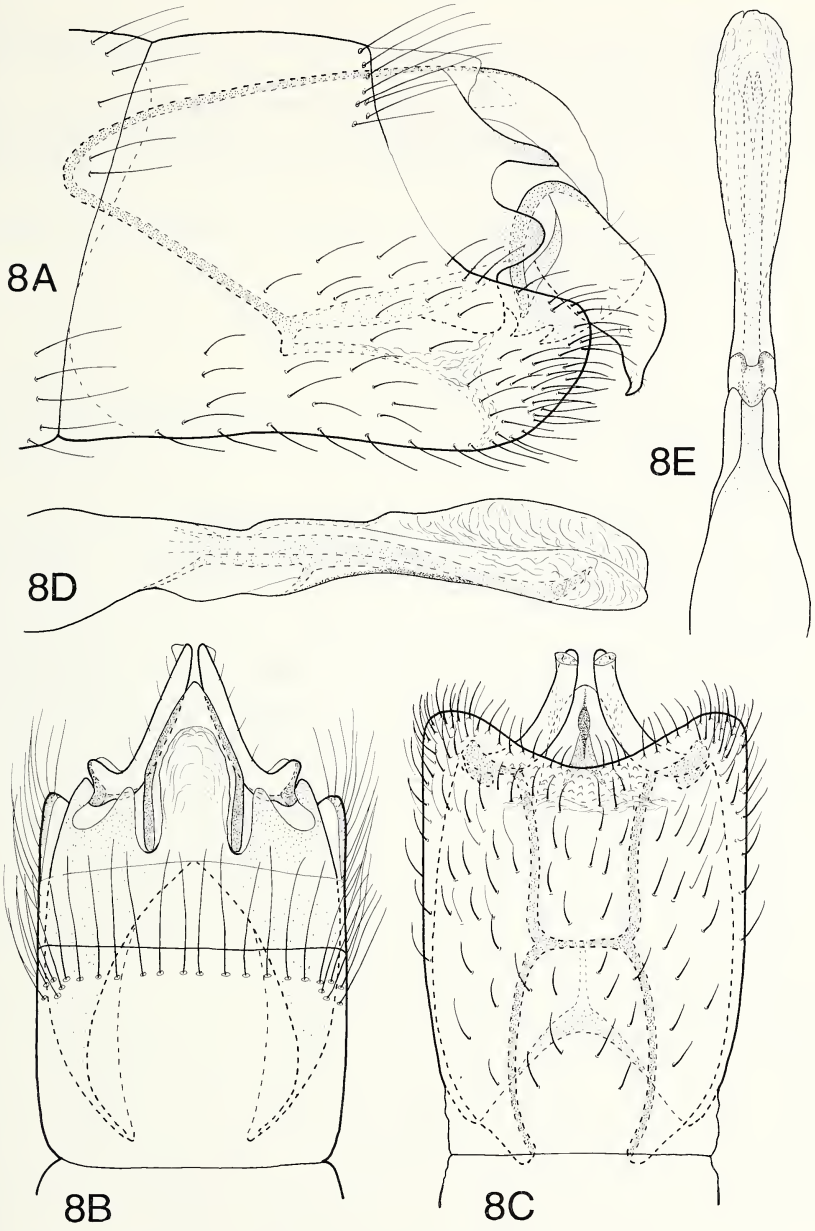


Fig. 8. *Byrsopteryx abrelata*, n. sp., male genitalia.

of segment VIII. Segment X short, triangular, bearing pair of thin papillae. Vaginal apparatus anteriorly with thin circular sclerite and narrow band with small mesal plate; membranous posteriorly.

Holotype: Male, BRASIL: RIO DE JANEIRO: Nova Friburgo, municipal water supply, 950 m, 24.iv.1977, C. M. and O. S. Flint, Jr. (MZSP). Paratypes: Same locality as holotype, 2 males, 3 females (NMNH), 2 males, 5 females (UMSP) (in alcohol).

Etymology: Portuguese and Spanish for "can-opener," referring to the shape of the dorsolateral process of segment IX of the male.

Byrsopteryx chaconi, new species
Figs. 6, 9, 26

The shape of the dorsolateral processes and the elongate thickened spines on the ventrolateral margin of male segment VIII are distinctive for *B. chaconi* as is the simple phallic apparatus, which lacks internal spines. The female vaginal apparatus has a very thin transverse band and thin sinuate lateral sclerites.

Male: Length 2.1–2.8 mm. Antennae with 17 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 9. Segment VIII roughly quadrate, tergum less than half length of sternum; laterally and ventrally with thickened, elongate setae; posterior margin with narrow, attenuated, strongly mesally turned, dorsolateral process, its apex excavated; VIII ventrolaterally with pair of long, stout, dark, spinelike setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, abruptly narrowing distally, bearing elongate basodorsal seta. Inferior appendages fused into narrow, elongate tube, in lateral view thin and slightly downturned. Segment X narrow basally, much broader mesally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally and subapically, pair of thin sclerites apically.

Female: Length 2.2–2.8 mm. Antennae with 19 segments. Coloration as in male. Genitalia as in Figure 26. Abdominal segment VII elongate, sternum with slightly emarginate posterior margin. Segment VIII narrow, posterior margin with ring of stout setae, laterally with pair of elongate apodemes extending to middle of segment VII. Segment IX short, narrow, with lateral apodemes extending to posterior of segment VII. Segment X short, wide basally, narrow distally, bearing pair of thin papillae. Vaginal apparatus with thin transverse band anteriorly, elongate posterior tubular process, slightly widening distally, pair of narrow, sinuate, lateral sclerites.

Holotype: Male, COSTA RICA: PUNTARENAS: roadside seep, route 2, just W km 234, 8.976°N, 83.299°W, 100 m, 8.iv.1987, Holzenthal, Hamilton, Heyn (NMNH). Paratypes: Same locality as holotype, 4 males, 4 females (UMSP), 1 female (UMSP) (in alcohol); same, except 20.ii.1986, Holzenthal, Morse, Fasth, 6 males, 9 females (UMSP), 2 males, 2 females (NMNH), 2 males, 2 females (INBIO), 30 males, 28 females (UMSP) (in alcohol).

Etymology: Named for Isidro Chacón, lepidopterist with the Museo Nacional de Costa Rica, in recognition of his great assistance and friendship during the junior author's work in Costa Rica.

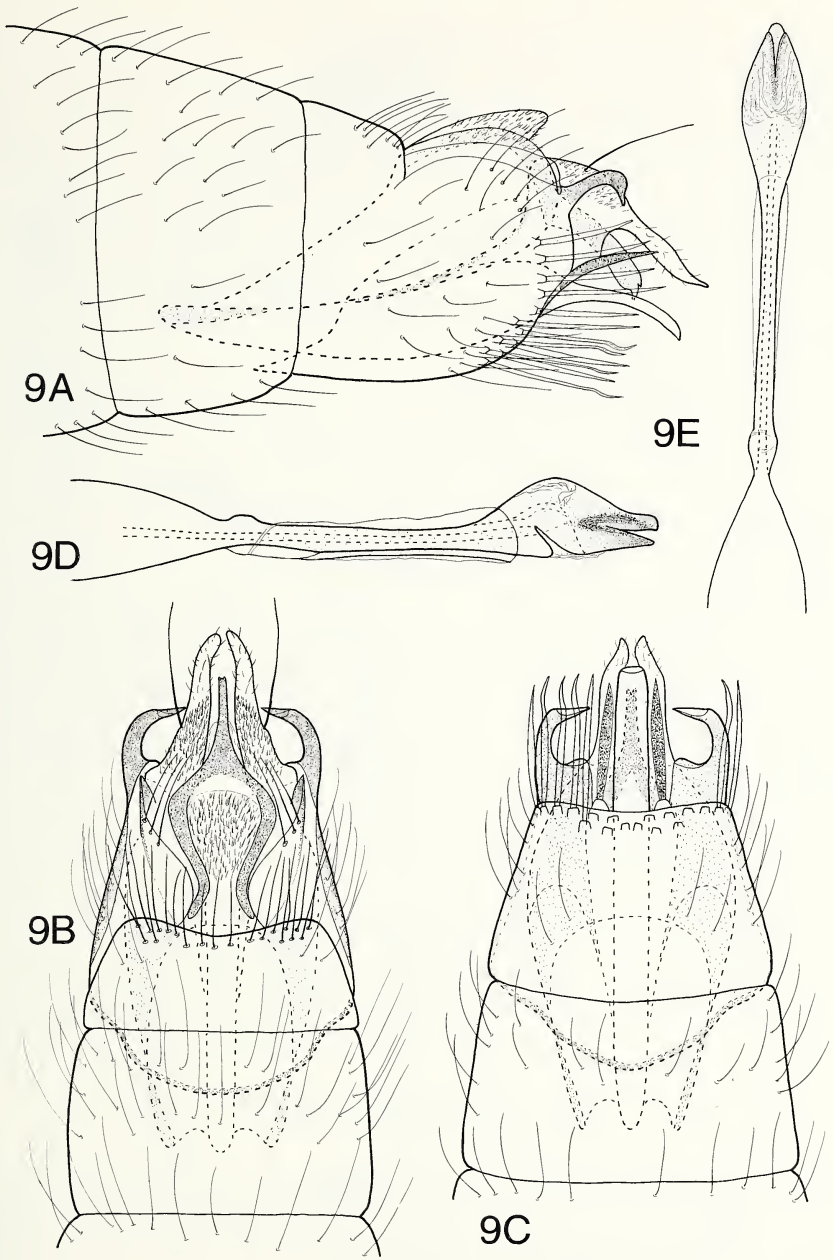


Fig. 9. *Byrsopteryx chaconi,* n. sp., male genitalia.

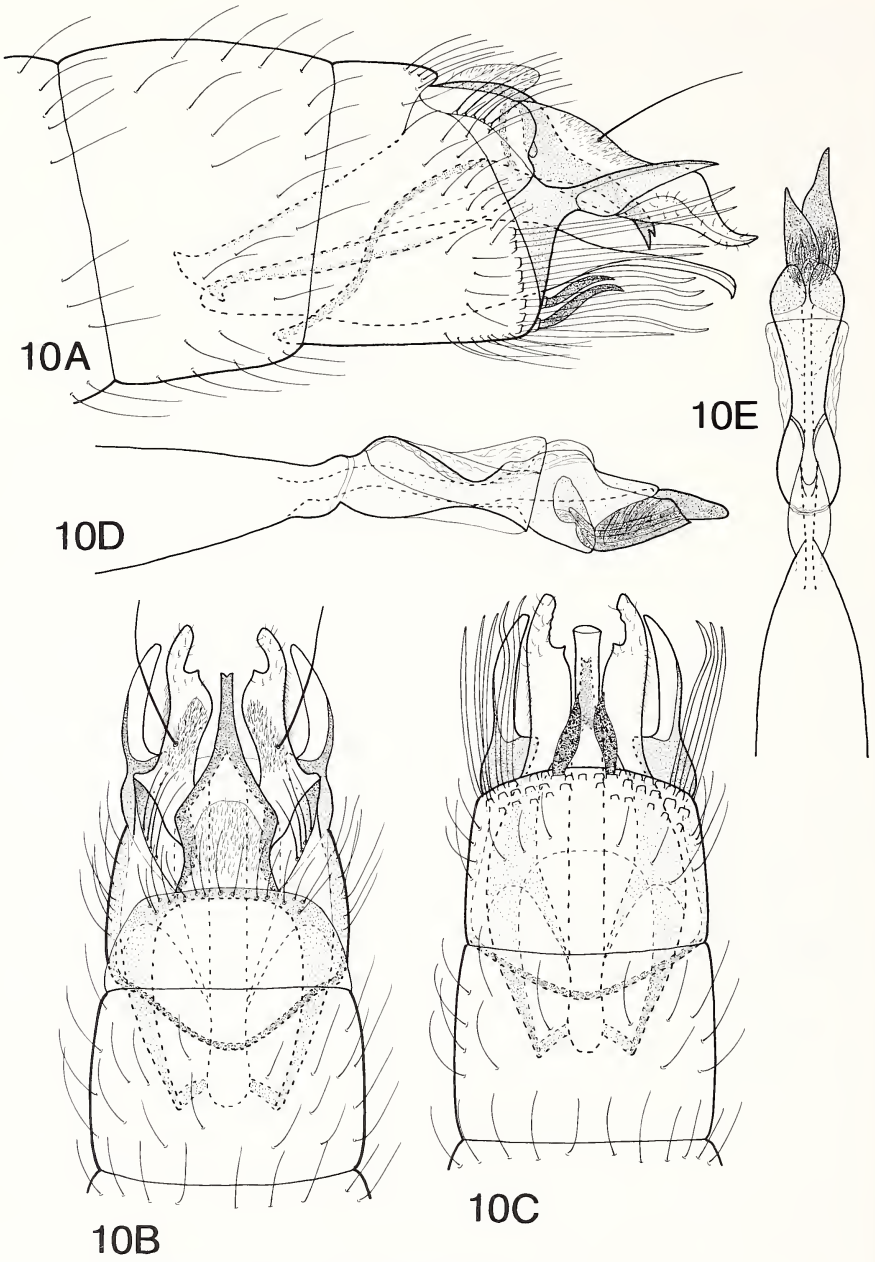


Fig. 10. *Byrsopteryx cuchilla,* n. sp., male genitalia.

Byrsopteryx cuchilla, new species
Figs. 10, 27

The knifeshaped dorsolateral processes of segment VIII and the short, thickened spines on the venter of VIII are distinguishing characters of the males of this species. The vaginal apparatus of the female has large oblong lateral plates and a wide transverse band.

Male: Length 2.3–2.7 mm. Antennae with 19 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 10. Segment VIII quadrate, tergum about half length of sternum; laterally and ventrally with thickened elongate setae; posterior margin with knifeshaped lateral process; VIII mesoventrally with pair of short, stout, dark, spinelike setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with sinuate, elongate, dorsolateral process, broad basally and mesally, narrowing distally, elongate basodorsal seta, in dorsal and ventral views dorsolateral process wide for ¾ length, then narrowing subapically, with small, subapicomesal, acute projection. Inferior appendages fused into elongate thin tube, in lateral view, wide basally, then narrowing to downturned apex. Segment X narrow basally, broader mesally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically, apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus structurally complex, wide basally, mesally and subapically; pair of large, lanceolate sclerites apically.

Female: Length 2.7 mm. Antennae with 19 segments. Coloration as in male. Genitalia as in Figure 27. Segment VII elongate, sternum with slightly emarginate posterior margin. Segment VIII elongate, narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, narrow, with lateral apodemes extending to middle of segment VII. Segment X short, wide basally, narrow distally, bearing pair of thin papillae. Vaginal apparatus with narrow transverse band anteriorly, with elongate, tubular, posterior process, slightly widening distally, laterally with pair of oblong lobes, sclerotized on anterior margins.

Holotype: Male, COSTA RICA: [CARTAGO]: Chitaría, 19.vi.1967, Flint and Ortiz (NMNH). Paratypes: Same locality as holotype, 4 males (NMNH), 1 male (UMSP), 1 male (INBIO), 1 female (NMNH) (in alcohol).

Etymology: Spanish for "knife" or "blade," referring to the distinctive dorsolateral processes from segment VIII of the male genitalia.

Byrsopteryx esparta, new species
Fig. 11

In many respects, *B. esparta* is similar to *B. cuchilla.* Males of both have knifelike dorsolateral processes from segment VIII, but the thickened spines from the ventrolateral margin of this new species are elongate.

Male: Length 2.2–2.4 mm. Antennae with 19 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 11. Segment VIII quadrate, tergum about ⅓ width of sternum; laterally and ventrally with thickened, elongate setae; posterior margin with narrow, knifeshaped, mesally directed, lateral process; VIII ventrolaterally with pair of long, narrow, dark, spinelike setae. Segment IX

recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views, posteriorly with elongate dorsolateral process, narrowing distally, bearing elongate, basodorsal seta; in dorsal view, lateral process wide basally, narrowing distally. Segment X narrow basally, broader mesally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Inferior appendages fused into elongate, narrow tube; in lateral view, wide basally, then narrowing to downturned apex. Subgenital plate absent. Phallic apparatus wide basally, tubular apically, apex with pair of thin, flat sclerites.

Female: Unknown.

Holotype: Male, COSTA RICA: [PUNTARENAS]: 14.1 mi SE Esparta, 23.vii.1967, O. S. Flint, Jr. (NMNH). Paratypes: Same locality as holotype, 11 males (NMNH); Puntarenas: Río Jaba at rock quarry, 1.4 km (air) W Las Cruces, 8.79°N, 82.97°W, 1,150 m, 9.viii.1990, Holzenthal, Blahnik, Muñoz, 16 males, 1 female (UMSP), 8 males (INBIO) (in alcohol).

Etymology: Named for the type locality, the small town of Esparta, east of the Pacific port city of Puntarenas.

Byrsopteryx espinhosa, new species
Fig. 12

The prominent dorsolateral process from segment IX with its acute projections and the numerous subapical phallic spines are distinctive features of *B. espinhosa.* The species is not clearly related to any others in the genus.

Male: Length 3.2 mm. Antennae with 17 segments, covered with white setae. Forewing coloration as in Figure 3, except apical spot larger. Legs, especially forelegs, with white setae along anterior edges. Genitalia as in Figure 12. Segment VIII quadrate, tergum shorter than sternum; posterior margin broadly rounded ventrolaterally, truncate ventrally and bearing long setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views, posteriorly with divided lateral process, its dorsal part elongate and downturned to acute apex, ventral part short and acute; in ventral view, dorsal part spatulate, ventral part short and wide with acute points on inner apical margins. Inferior appendages appear to be absent. Segment X broad, largely membranous, without setae; sclerotized laterally. Subgenital plate truncate in ventral view with small apicomesal projection, in lateral view, oblong in shape, the apicomesal projection downturned. Phallic apparatus structurally complex, wide basally, tubular distally, with dorsolateral sclerotization and numerous subapical spines.

Female: Unknown.

Holotype: Male, BRASIL: RIO DE JANEIRO: km 17, 18 km S Teresopolis, 1,180 m, 18–19.iv.1977, C. M. and O. S. Flint, Jr. (MZSP).

Etymology: Portuguese for "thorny" or "prickly," in reference to the phallic spines.

Byrsopteryx gomezi, new species
Figs. 3, 13, 24

This new species is closely related to the other Costa Rican species. The lack of a prominent dorsolateral process from the posterior margin of male segment VIII and

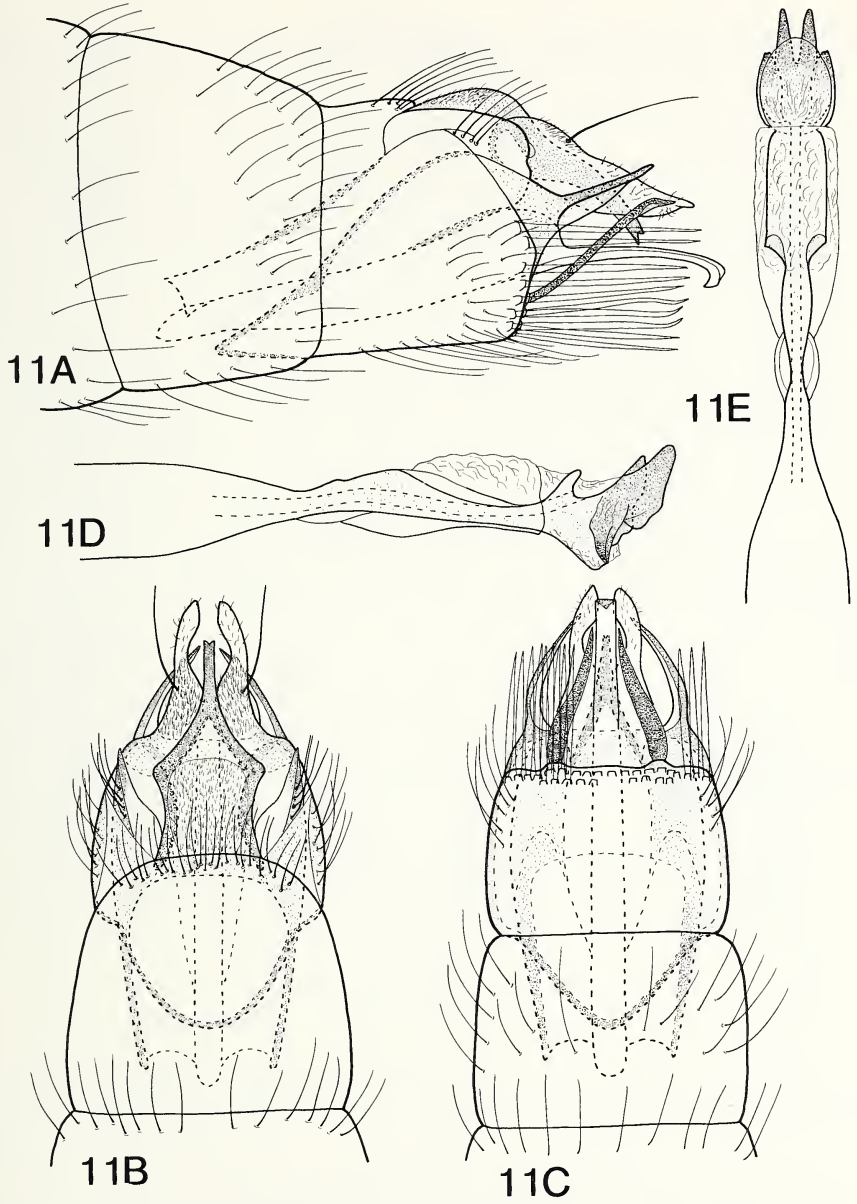


Fig. 11. *Byrsopteryx esparta,* n. sp., male genitalia.

the distinctive spinose phallic apparatus serve to distinguish *B. gomezi* from its relatives. The female is easily distinguished by the large membranous anterior lobes and elongate posterior tubular process of the vaginal apparatus.

Male: Length 2.3–2.5 mm. Antennae with 17 segments. Forewing coloration as in

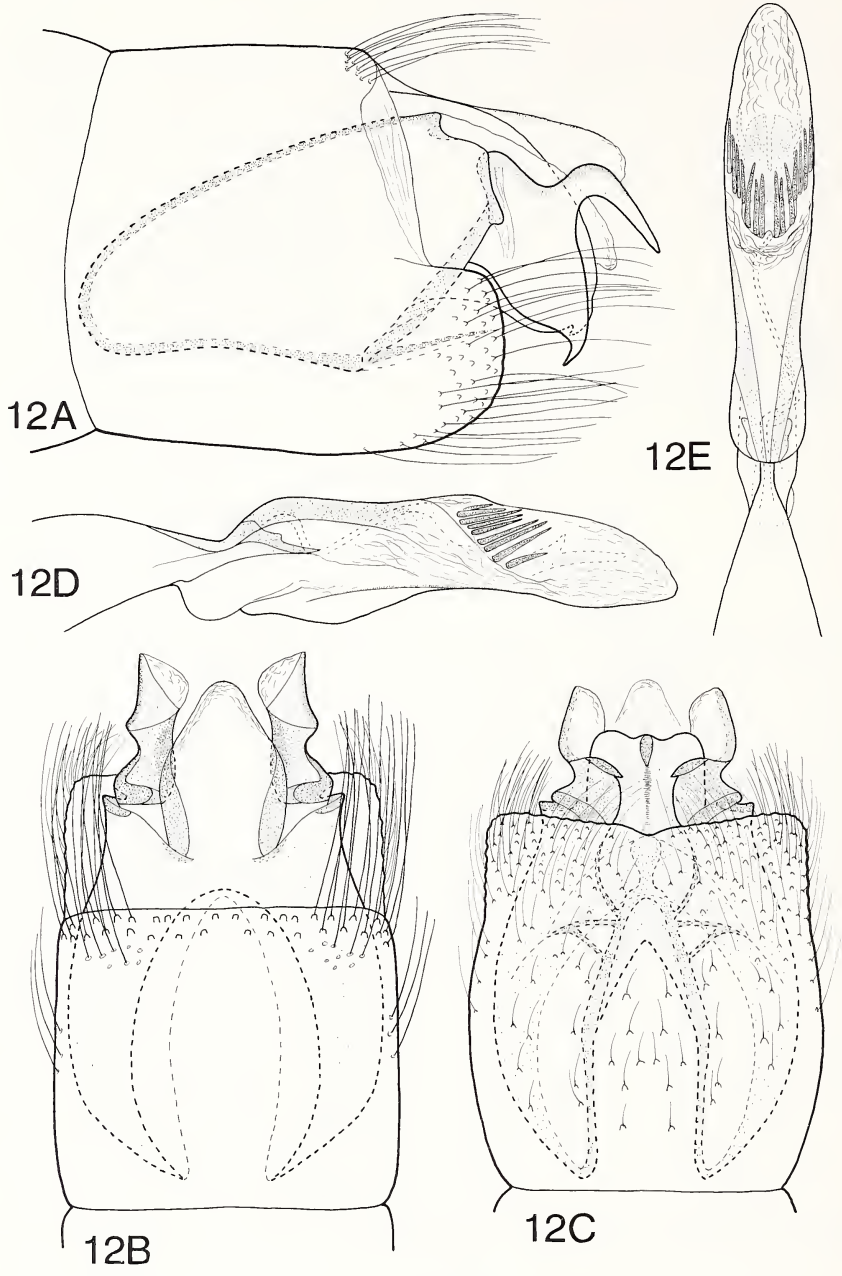


Fig. 12. *Byrsopteryx espinhosa*, n. sp., male genitalia.

Figure 3. Legs without white setae. Genitalia as in Figure 13. Segment VIII roughly quadrate, tergum shorter than sternum; posterior margin broadly rounded ventrolaterally and ventrally and bearing many thickened, elongate setae. Segment IX elongate, recessed within segments VIII and VII, acutely narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate sinuate lateral process, broad basally, narrowing distally, bearing elongate seta middorsally. Inferior appendages fused into elongate, narrow tube; in lateral view, thin, slightly downturned. Segment X broad basally, membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, narrow mesally, distally bearing clump of mesal spines, with pair of elongate, thickened lateral spines, apex divided into pair of long, spinose lobes.

Female: Length 2.3–2.5 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 24. Segment VII elongate. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VI. Segment IX short with lateral apodemes extending to middle of segment VIII. Segment X short, wide basally narrowing apically, bearing pair of thin papillae. Vaginal apparatus with pair of elaborate, membranous lobes anteriorly, oblong mesal plate with elongate tubular process posteriorly.

Holotype: Male, COSTA RICA: PUNTARENAS: Río Bellavista, ca. 1.5 km NW Las Alturas, 8.951°N, 82.846°W, 1,400 m, 10–11.viii.1990, Holzenthal, Blahnik, Muñoz (NMNH). Paratypes: Same locality as holotype, 98 males, 1 female (UMSP). ALAJUELA: Río Peje and falls, ca. 1 km SE San Vicente, 10.277°N, 84.388°W, 1,450 m, 14–15.ii.1992, Holzenthal, Muñoz, Kjer, 24 males, 2 females (UMSP). CARTAGO: Orosí, Río Tuasito, 1,200 m, L-N-196300, 565200, 14.ix.1991, F. Muñoz, F. A. Quesada, 8 males, 1 female (INBIO). GUANACASTE: Río Aguacate, 0.5 km E Aguacate, 10.565°N, 84.939°W, 16.ii.1992, Holzenthal, Muñoz, Kjer, 6 females (UMSP).

Etymology: Named for Luís Diego Gómez, eminent Costa Rican biologist, both in honor of his pioneering contributions to our knowledge of Costa Rican natural history and in recognition of his invaluable assistance to the junior author.

Byrsopteryx loja, new species
Figs. 14, 21

The acute divided lateral process of segment IX and elongate central phallic spine are distinguishing features of male *B. loja.* The female is recognized by the tapered ventral process of segment IX and the shape of the vaginal apparatus, which it shares with *B. rayada,* n. sp.

Male: Length 2.4–3.0 mm. Antennae with 17 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 14. Segment VIII with tergum about half length of sternum; posterior margin narrowly rounded and extended ventrolaterally, bearing long setae; ventally with small, shallow mesal incision. Segment IX recessed within VIII, narrowing anteriorly in lateral view, narrow mesal incision anteriorly in ventral view, posteriorly with divided sclerotized lateral process, divided into dorsal and ventral subprocesses, dorsal subprocess elongate and narrow, with acute, downturned apex, ventral subprocess wide basally with narrow ventral

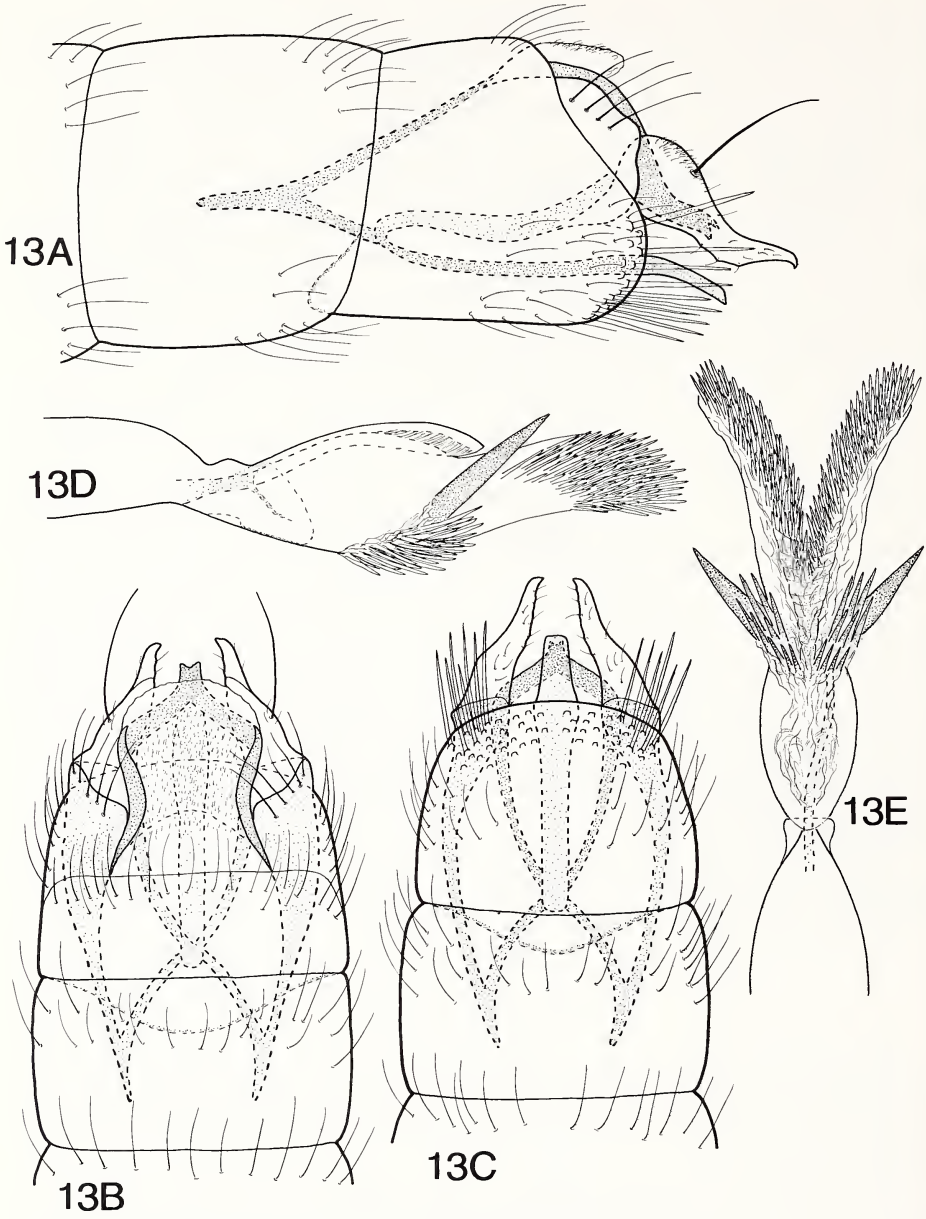


Fig. 13. *Byrsopteryx gomezi,* n. sp., male genitalia.

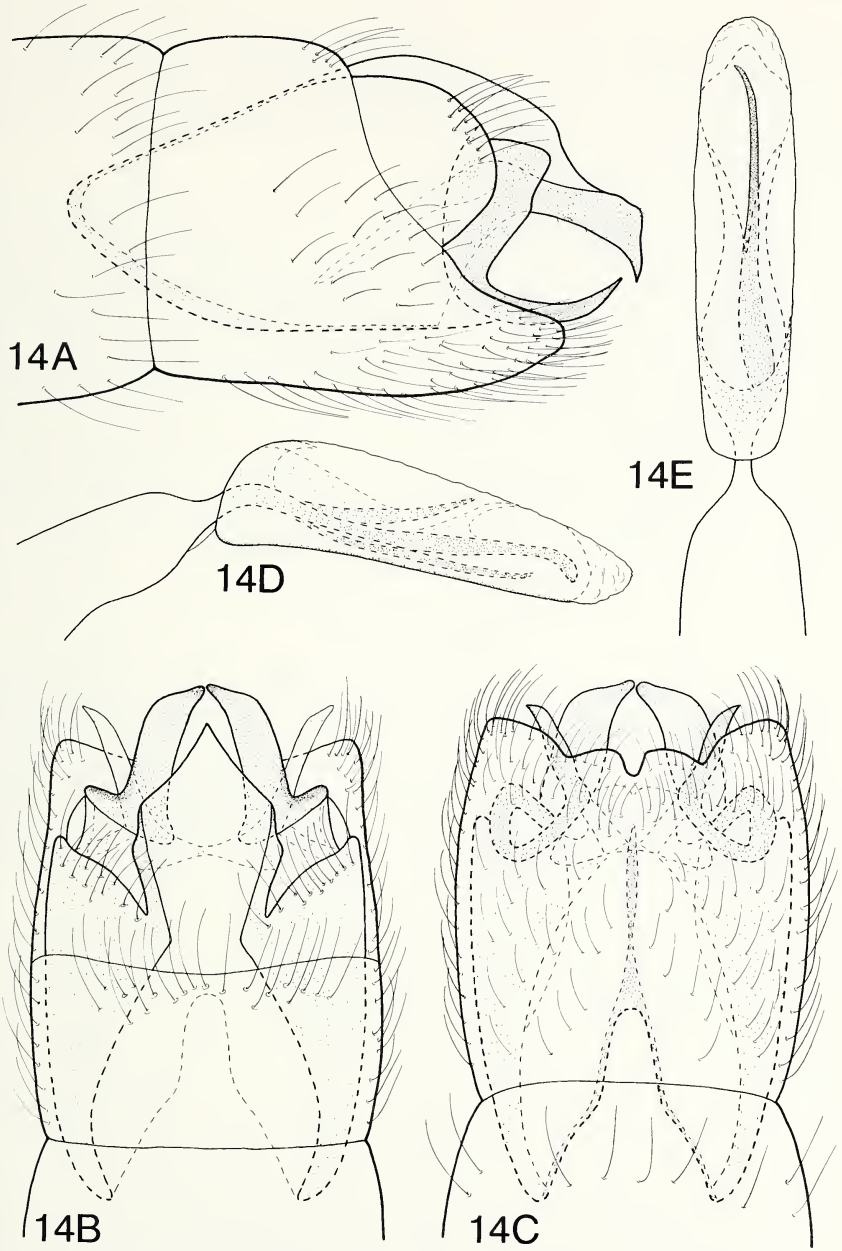


Fig. 14. *Byrsopteryx loja,* n. sp., male genitalia.

hook, in ventral view this hook thin, directed outward, dorsal subprocess wide, apex narrow, turned mesally. Inferior appendages absent. Segment X broad, largely membranous, narrowing to acute apex; sclerotized laterally. Subgenital plate narrow and oblique in lateral view, rectangular in ventral view. Phallic apparatus somewhat simple, wide basally, tubular distally, with thin elongate central spine and pair of lateral sickle-shaped sclerites.

Female: Length 2.4 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 21. Segment VI with short ventromesal process. Segment VII about as wide as long. Segment VIII elongate, narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX elongate, narrow, ventrally with tapering process, laterally with pair of elongate apodemes extending to posterior of segment VII. Segment X short, wide basally, narrow distally, bearing pair of thin papillae. Vaginal apparatus structurally simple, thin transverse band and lateral sclerotization anteriorly, posteriorly with membranous foldings.

Holotype: Male, ECUADOR: ZAMORA-CHINCHIPE: 30 km E Loja, 2,000 m, 23.ix.1990, O. S. Flint, Jr. (NMNH). Paratypes: Same locality as holotype, 2 males (NMNH), 1 male (UMSP), 19 males, 1 female (NMNH) (in alcohol).

Etymology: Named for the city of Loja, near the type locality.

Byrsopteryx mirifica Flint
Figs. 5, 15, 23

Byrsopteryx mirifica Flint, 1981:27, figs. 121–126, male, Venezuela: Aragua, USNM type 76625; Holzenthal and Harris, 1992:405, figs. 1, 2, male, female, larva, case.

Byrsopteryx mirifica is similar in some respects to *B. loja* in that the posterior processes from male segment IX are bifurcate and the phallic apparatus is rather simple, but the two species do not appear to be closely related. The long spinose process from the venter of X is distinctive for the species. The females are easily distinguished by the large mesal plate and the large posterior membranous lobes of the vaginal apparatus.

Redescription: Male: Length 2.3–2.6 mm. Antennae with 17 segments. Transverse white band on head above antennal bases, pair of round white spots on mesoscutum, elongate white spot basally on forewing, oblique spot near midlength, and series of small apical spots around wing margin. Genitalia as in Figure 15. Segment VIII roughly quadrate, tergum about half length of sternum; round and extended ventrolaterally, ventrally with V-shaped mesal incision. Segment IX short, recessed within VIII, rounded anteriorly in lateral view; deep mesal incision anteriorly in dorsal and ventral views, posteriorly with divided lateral processes, each of which is narrow and elongate; in ventral view, these processes appearing chelate. Inferior appendages fused, thin, curving ventrad in lateral view; in ventral view wide basally tapering to thin, downturned apex, curving ventrad. Segment X largely membranous, short; apparently associated with X dorsomesally is a long, thin, gently curved sclerotized process (fused intermediate appendages?). Subgenital plate reduced, represented by pair of mesal crescentric sclerites. Phallic apparatus simple, tubular, narrowing mesally, ejaculatory duct thin with sclerotized apex.

Female: Length 2.4–2.6 mm. Antennae with 17 segments. Coloration as in male.

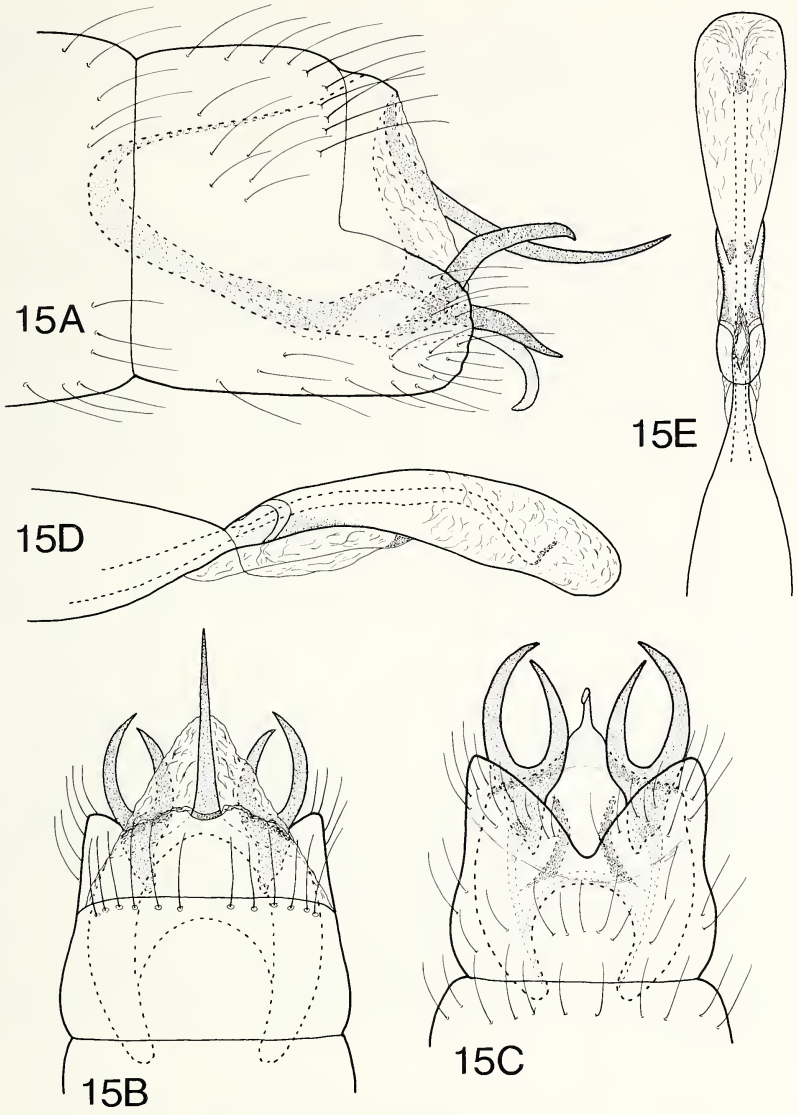


Fig. 15. *Byrsopteryx mirifica* Flint, male genitalia.

Genitalia as in Figure 23. Segment VII elongate, sternum incised mesally on posterior margin. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short with lateral apodemes extending to posterior of segment VII. Segment X short, wide, narrowing posteriorly, bearing pair of thin papillae. Vaginal apparatus with pair of large membranous lobes posteriorly; lightly sclerotized mesal plate, with wide mesal excision posteriorly, narrow tongue anteriorly.

Material examined: VENEZUELA: ARAGUA: Parque Nacional Henri Pittier, Río La Trilla, 22.5 km N Rancho Grande on road, 17–19.ix.1979, H. M. Savage, 1 male (NMNH); Maracay, Río Limón, Estacion Piscicultura, 16.ii.1976, C. M. and O. S. Flint, Jr., 25 male paratypes, 10 female paratypes (NMNH).

Byrsopteryx rayada, new species
Figs. 4, 7, 16, 22

The distinctive white bands on the forewings, the lobate lateral process of segment IX of the male, and the overall large size separate the new species. The vaginal apparatus of the female is simple and most similar to that of *B. loja.*

Male: 3.2–4.8 mm. Antennae with 17 segments, covered with white setae. Forewing coloration as in Figures 4, 7. Genitalia as in Figure 16. Segment VIII with tergum shorter than sternum; posterior margin broadly rounded and extended ventrolaterally, with V-shaped mesal excavation ventrally and bearing long setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views, posteriorly with elongate lateral process divided into lateral and mesal subprocesses, lateral subprocess broad basally, abruptly narrowing to blunt ventral lobe, mesal subprocess elongate, narrow, with downturned acute apex. Inferior appendages absent. Segment X broad, largely membranous, sclerotized laterally, apex acute and downturned. Subgenital plate absent. Phallic apparatus wide basally, tubular distally, with thin, curving, elongate central spine and membranous apical lobes.

Female: Length 3.8 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 22. Segment VI with short ventromesal process. Segment VII quadrate. Segment VIII elongate, narrow, posterior margin with ring of stout setae, laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, wide, deeply incised ventrally, with pair of elongate mesal apodemes extending to posterior of segment VII. Segment X short, wide basally, narrow distally, with pair of thin papillae. Vaginal apparatus structurally simple, with thin transverse band anteriorly, posteriorly with membranous foldings, tapered distally.

Holotype: Male, ECUADOR: CAÑAR: Río Chauchas, 3 km N Zhud, 2,910 m, 17.ix.1990, O. S. Flint, Jr. (NMNH). Paratypes: Same locality as holotype, 17 males, 1 female (NMNH), 2 males (UMSP), 2 males (NMNH) (in alcohol).

Etymology: Spanish, meaning "having stripes" and referring to the distinctive, striped forewings.

Byrsopteryx septempunctata (Flint)
Fig. 17

Alisiotrichia septempunctata Flint, 1968:46, figs. 106–109, male, Dominica: Pont Casse, USNM Type 69898; *Byrsopteryx septempunctata,* Flint, 1981:27.

Byrsopteryx septempunctata is distinguished by its combination of genitalic features, including the inferior appendages which are fused into a thin elongate tubular process, the venter of segment X which is less developed than in many *Byrsopteryx* species, and the paired lateral processes of segment IX. It seems to be the sister species of the Costa Rican clade.

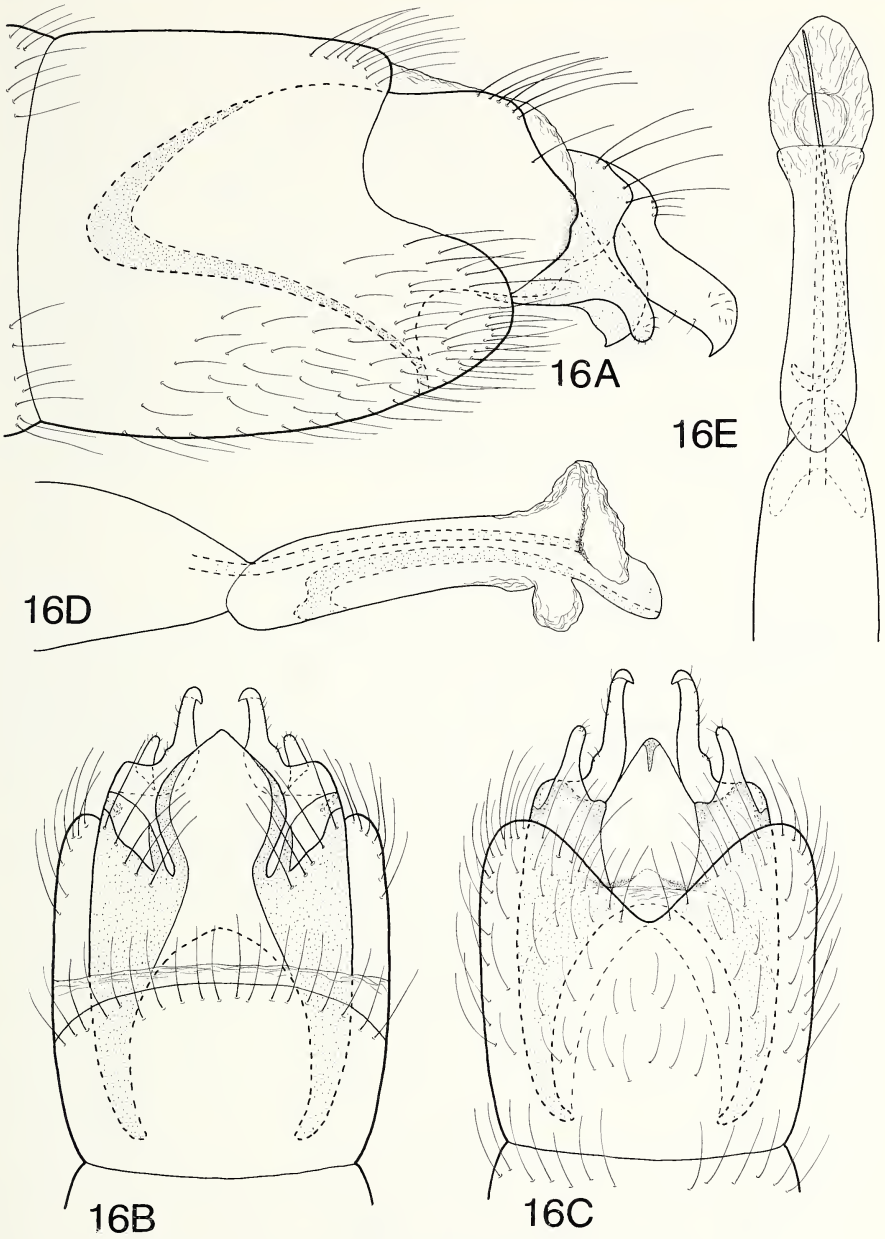


Fig. 16. *Byrsopteryx rayada,* n. sp., male genitalia.

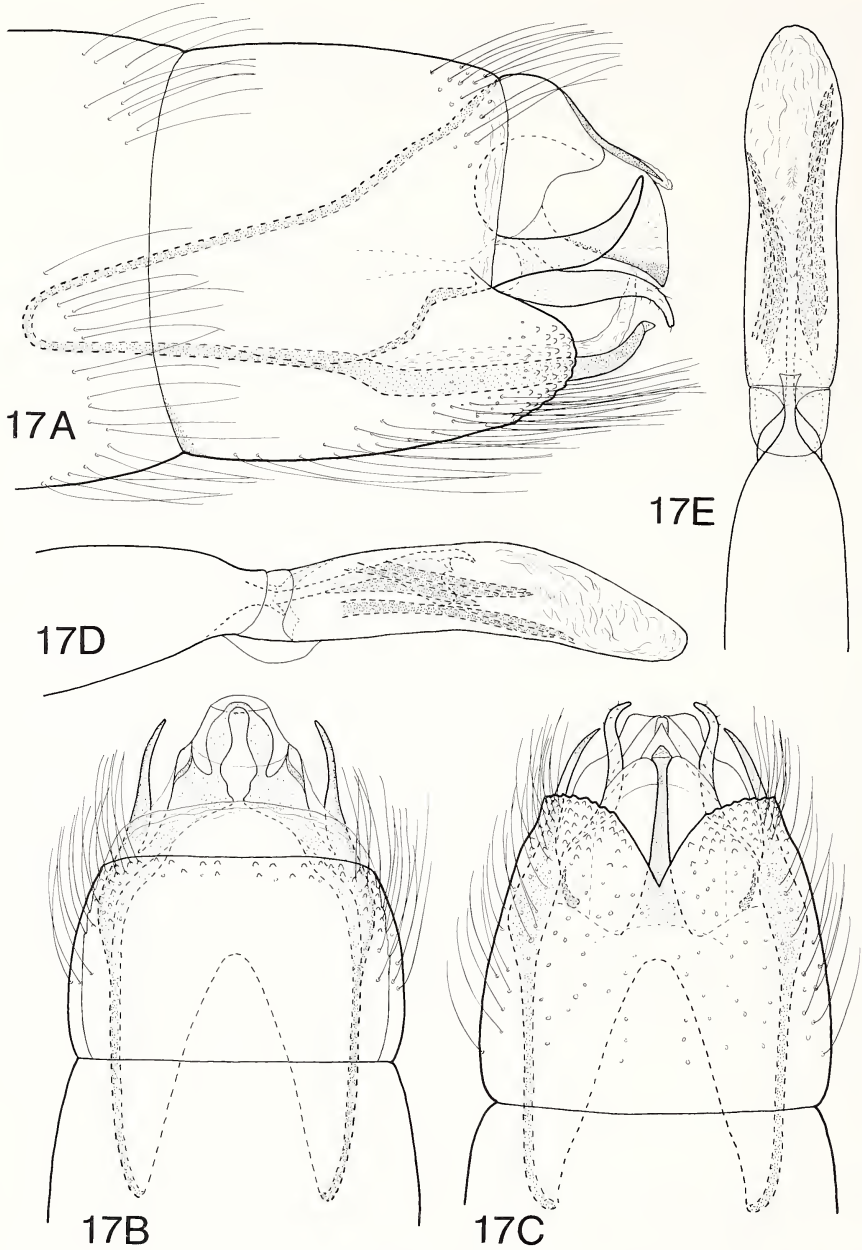


Fig. 17. *Byrsopteryx septempunctata* (Flint), male genitalia.

Redescription: Male: Length 2.6 mm. Antennae with 17 segments. Forewing coloration as in Figure 6, except spots bright green. Genitalia as in Figure 17. Segment VIII quadrate, tergum shorter than sternum; posterior margin rounded ventrolaterally, ventrally with V-shaped mesal incision; bearing many long setae. Segment IX elongate, recessed within VIII, narrowing anteriorly in lateral view; deep mesal incision anteriorly in dorsal and ventral views; posteriorly with pair of thin lateral processes, upper process upturned, lower process downturned, in ventral view upper process more lateral in position, narrow and acute apically, lower process mesad in position, sinuate distally. Inferior appendages fused into elongate, narrow tube, membranous laterally; in lateral view, thin, upturned apically. Segment X membranous anterodorsally, posteriorly with sclerotized lateral bands; venter sclerotized. Subgenital plate absent. Phallic apparatus wide basally, narrow mesally, cylindrical distally with 6–7 elongate, curved, internal spines.

Female: Unknown.

Material examined: DOMINICA: Pont Casse, 2.2 mile east, 14.iv.1964, O. S. Flint, Jr., holotype male, USNM Type 69898.

Byrsopteryx solisi, new species
Figs. 18, 28

The truncate dorsolateral process and the four thick elongate spines from the ventromesal margin of segment VIII are distinguishing male characteristics for this species. The female vaginal apparatus has an elongate posterior tubular process, small oblong lateral plates, and a wide transverse band.

Male: Length 2.4–2.8 mm. Antennae with 19 segments. Forewing coloration as in Figure 3. Legs without white setae. Genitalia as in Figure 18. Segment VIII quadrate, tergum shorter than sternum; posterior margin with broad, blunt, dorsolateral process; ventrolaterally with thickened, elongate setae; mesoventrally VIII somewhat narrowed distally and bearing 4 stout, dark, spinelike setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, deep mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, narrowing and downturned distally, bearing elongate seta basodorsally. Inferior appendages fused into short tube; in ventral view wide basally, slightly tapering distally; in lateral view thin, gently downturned. Segment X narrow basally, broader mesally; membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, very narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, tubular distally, bearing pair of large, lanceolate spines apicoventrally.

Female: Length 2.6–3.1 mm. Antennae with 19 segments. Coloration as in male. Genitalia as in Figure 28. Segment VII elongate, sternum slightly emarginate on posterior margin. Segment VIII narrow, posterior margin emarginate with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short with lateral apodemes extending to middle of segment VIII. Segment X short, widest mesally, bearing pair of thin papillae. Vaginal apparatus with narrow transverse band mesally, tubular processes posteriorly, pair of lightly sclerotized oblong plates laterally, truncate anteriorly.

Holotype: Male, COSTA RICA: PUNTARENAS: Río Singrí, 2 km (air) S Finca

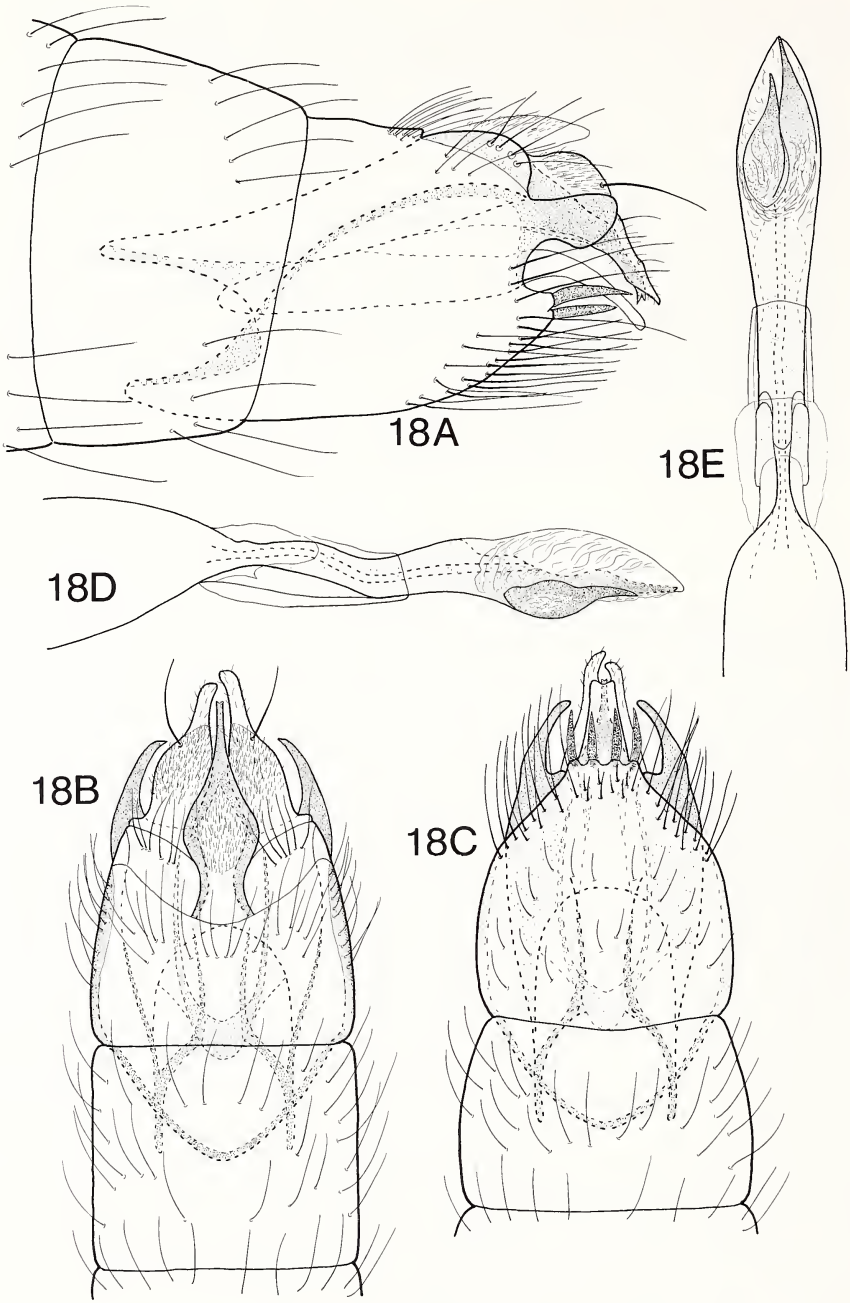


Fig. 18. *Byrsopteryx solisi,* n. sp., male genitalia.

Helechales, 9.057°N, 83.082°W, 720 m, 21.ii.1986, Holzenthal, Morse, Fasth (NMNH). Paratypes: Same locality as holotype, 26 males, 16 females (UMSP). ALAJUELA: Río Sarapiquí, ca. 2 km SE Cariblanco, 10.299°N, 82.172°W, 710 m, 22.vi.1986, Holzenthal, Heyn, Armitage, 3 males, 1 female (INBIO). GUANACASTE: Río Aguacate, 0.5 km E Aguacate, 10.565°N, 84.939°W, 16.ii.1992, Holzenthal, Muñoz, Kjer, 1 male (UMSP). HEREDIA: Río Bijagual on road to Magsasay, 10.408°N, 84.076°W, 140 m, 12.ii.1986, Holzenthal, Morse, Fasth, 1 male (NMNH). PUNTARENAS: Río Guineal, ca. 1 km (air) E Finca Helechales, 9.076°N, 83.092°W, 840 m, Holzenthal, Morse, Fasth, 18 males, 7 females (UMSP).

Etymology: Named in honor of Angel Solís, curator of Coleoptera and head of the Department of Entomology, Instituto Nacional de Biodiversidad, Costa Rica, who has been instrumental in the initial and continued success of the junior author's research in Costa Rica.

Byrsopteryx tapanti, new species
Figs. 19, 29

The elongate, narrow dorsolateral processes and pair of thickened spines from the ventrolateral margin of segment VIII are distinctive for males of *B. tapanti.* The female vaginal apparatus has a thin, sinuate posterior process originating from an oblong mesal plate.

Male: Length 2.7–3.0 mm. Antennae with 17 segments. Forewing coloration as in Figure 3. Legs without white setae. Genitalia as in Figure 19. Segment VIII roughly quadrate, tergum less than half length of sternum; posterior margin with thin, elongate dorsolateral process, sharply bent downward at apex, curved inward when viewed ventrally; ventrolaterally with pair of long, stout spines, slightly curved inward apically; mesoventrally with pair of thin spines, these sinuate in lateral view, straight in ventral view; VIII laterally and ventrally with thickened, elongate setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, narrowing and downturned distally, bearing elongate seta basodorsally. Inferior appendages fused into narrow, elongate tube; in lateral view thin, gently downturned. Segment X narrow basally, broader mesally; membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, tubular distally, bearing pair of spines apicoventrally and semimembranous, cone-shaped mesal protuberance.

Female: Length 2.7–3.0 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 29. Segment VII elongate, sternum slightly emarginate on posterior margin. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, narrow, with lateral apodemes extending to posterior of segment VII. Segment X short, widest mesally, bearing pair of thin papillae. Vaginal apparatus with thin, sinuate, transverse band anteriorly, oblong mesal plate bearing thin, elongate, tubular process posteriorly.

Holotype: Male, COSTA RICA: CARTAGO: Res. Tapantí, Quebrada Palmitos and falls, 9.72°N, 83.78°W, 1,400 m, 24–25.iii.1991, Holzenthal, Muñoz, Huisman

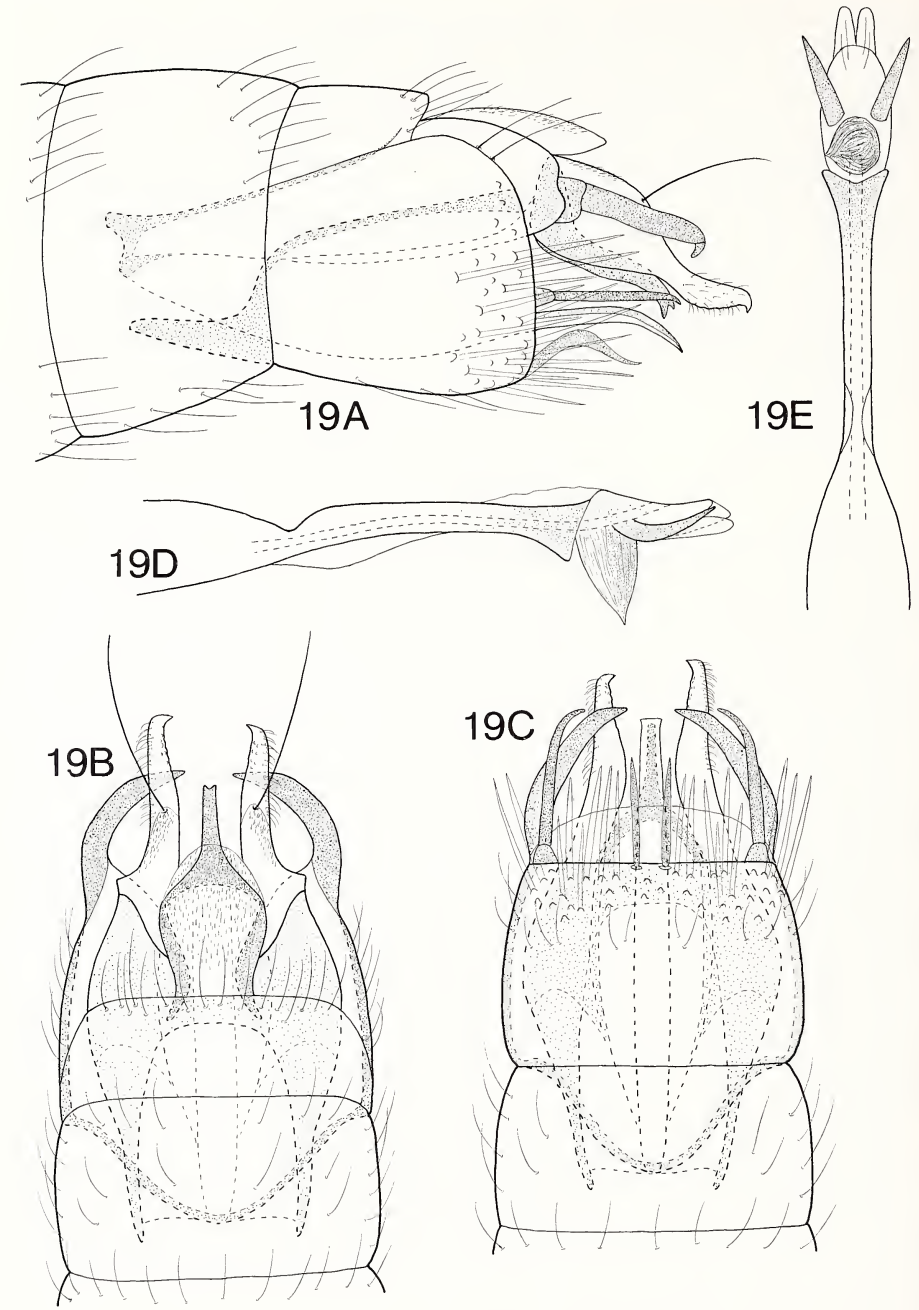


Fig. 19. *Byrsopteryx tapanti,* n. sp., male genitalia.

(NMNH). Paratypes: Same locality as holotype, 42 males, 1 female (UMSP); same, except 1–2.viii.1990, Holzenthal, Blahnik, Muñoz, 1 female (INBIO); same, except waterfall ca. 1 km (road) NW tunnel, 9.69°N, 83.76°W, 1,600 m, 24.iii.1991, Holzenthal, Muñoz, Huisman, 1 female (UMSP); same, except Q. Salto [=Q. Palmitos], 12.ix.1991, L-N-190650, 560000, F. Muñoz & F. A. Quesada, 2 males (INBIO).

Etymology: Named for the type locality, the Tapantí wildlife refuge near the town of Orosi, Cartago Province.

Byrsopteryx tica, new species
Figs. 20, 30

The thickened, curved spines from the posterior margin of male segment VIII are distinctive for *B. tica.* The female vaginal apparatus has a narrow transverse sclerite and elongated tubular process projecting posteriorly.

Male: Length 2.8–3.0 mm. Antennae with 17 segments. Forewing coloration as in Figure 6. Legs without white setae. Genitalia as in Figure 20. Segment VIII roughly quadrate, tergum less than half length of sternum; posterior margin with elongate dorsolateral process, downturned and sharply turned inward apically; ventrolaterally with pair of long, stout spines, strongly curved outward apically; VIII laterally and ventrally with thickened, elongate setae. Segment IX recessed within VIII, narrowing anteriorly in lateral view, broad mesal incision anteriorly in dorsal and ventral views; posteriorly with elongate dorsolateral process, broad basally, narrowing and downturned distally, bearing elongate seta basodorsally. Inferior appendages fused into narrow, elongate tube; in lateral view thin, gently downturned. Segment X narrow basally, broader mesally; membranous dorsally, the membrane covered with minute setae; sclerotized laterally and apically; apex of X bifid, narrow, downturned. Subgenital plate absent. Phallic apparatus wide basally, mesally, and subapically, bearing pair of spines apicoventrally and pair of membranous lobes apically.

Female: Length 2.8–3.0 mm. Antennae with 17 segments. Coloration as in male. Genitalia as in Figure 30. Segment VII elongate, sternum truncate on posterior margin. Segment VIII narrow, posterior margin with ring of stout setae; laterally with pair of elongate apodemes extending to anterior of segment VII. Segment IX short, narrow, with lateral apodemes extending to middle of segment VII. Segment X short, wide basally, narrowing to rounded apex, bearing pair of thin papillae. Vaginal apparatus with narrow transverse band anteriorly, elongate, tubular process posteriorly, widest basally and apically.

Holotype: Male, COSTA RICA: CARTAGO: Res. Tapantí, unnamed trib., ca. 8 km (rd.) S headquarters, 9.76°N, 83.78°W, 1,540 m, 24.iii.1991, Holzenthal, Muñoz, Huisman (NMNH). Paratypes: Same locality as holotype, 14 males, 2 females (UMSP), 1 male (INBIO), 1 male (NMNH).

Etymology: Named for the Costa Ricans, or "Ticos."

PHYLOGENETIC ANALYSIS

Methods. The computer program PAUP, version 3.1.1 (Swofford, 1993) was used to infer the phylogenetic relationships of the species of *Byrsopteryx.* The application was run on a Macintosh Centris 610® microcomputer with 16MB of RAM. Nineteen characters from larval and adult stages were included in the analysis. Characters were

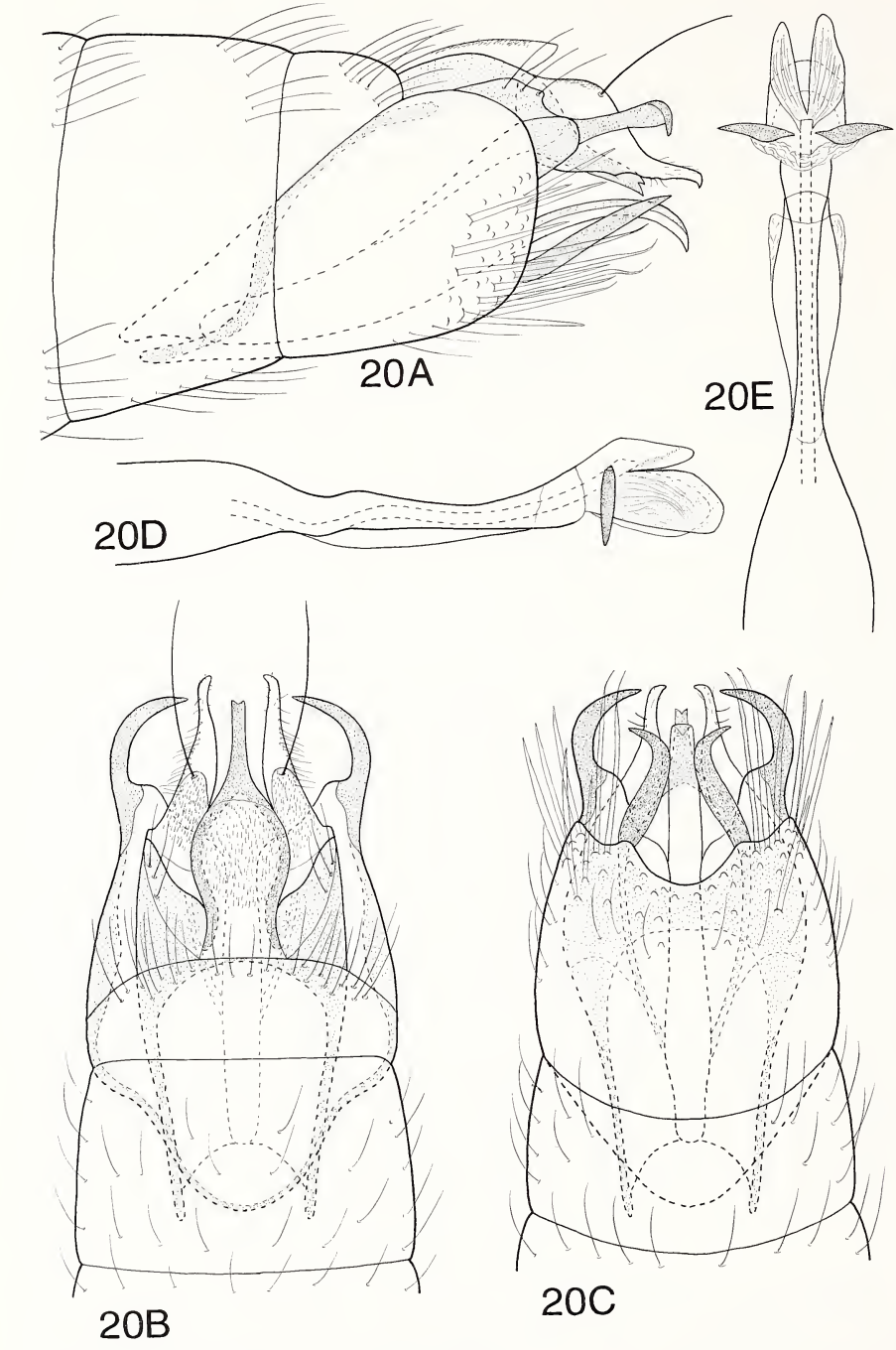


Fig. 20. *Byrsopteryx tica,* n. sp., male genitalia.

Table 1. Character matrix for *Byrsopteryx* species.

Taxa	Character																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Celaenotrichia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
abrelata	?	1	1	1	1	1	0	0	0	1	0	0	0	1	1	0	0	0	0
chaconi	1	1	1	1	1	1	1	1	1	2	1	1	1	1	0	1	2	1	0
cuchilla	?	1	1	1	1	1	1	2	1	2	1	1	1	1	0	1	1	1	0
esparta	?	1	1	1	1	1	1	2	1	2	1	1	1	?	?	?	?	?	?
espinhosa	?	1	1	1	1	1	0	0	0	0	0	0	0	?	?	?	?	?	?
gomezi	?	1	1	1	1	1	1	0	0	2	1	1	1	1	1	1	0	0	0
loja	?	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1
mirifica	1	1	1	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0
rayada	?	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1
septempunctata	?	1	1	1	1	1	0	0	0	0	0	1	1	?	?	?	?	?	?
solisi	?	1	1	1	1	1	1	1	1	2	1	1	1	1	0	1	1	1	0
tapanti	?	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	2	0	0
tica	?	1	1	1	1	1	1	1	1	2	1	1	1	1	0	1	1	1	0

Characters (0 = plesiomorphic state; 1, 2 = apomorphic states; ? = missing data): *Larval Character:* Character 1: 0 = larval pronotum normal; 1 = larval pronotum with lacunate areas and with strong apicolateral seta. *Adult Characters:* Character 2: 0 = forewing not punctate; 1 = forewing with bright white spots. Character 3: 0 = wing venation normal; 1 = wing venation reduced. Character 4: 0 = forewing without fracture; 1 = forewing with fracture. Character 5: 0 = 1, 3, 4 tibial spur formula; 1 = 0, 3, 4 tibial spur formula. *Male Genitalia:* Character 6: 0 = segment VII with ventromesal process; 1 = segment VII without ventromesal process. Character 7: 0 = segment VIII without long thick setae ventrally; 1 = segment VIII with long thick setae ventrally. Character 8: 0 = segment VIII without dorsolateral process; 1 = segment VIII with dorsolateral process; 2 = segment VIII dorsolateral process bladelike. Character 9: 0 = segment VIII without thick, spinelike mesoventral setae; 1 = segment VIII with thick, spinelike mesoventral setae. Character 10: 0 = segment IX with bifid posterolateral appendagelike process; 1 = segment IX with single, sinuate posterolateral appendagelike process; 2 = segment IX posterolateral appendagelike process single, sinuate, and with dorsal seta. Character 11: 0 = segment X unmodified; 1 = segment X with lyre-shaped sclerotization. Character 12: 0 = inferior appendages absent; 1 = inferior appendages present, but fused, tubular. Character 13: 0 = subgenital plate present; 1 = subgenital plate absent. *Female Genitalia:* Character 14: 0 = segment VI with ventromesal process; 1 = segment VI without ventromesal process. Character 15: 0 = vaginal apparatus without mesal plate; 1 = vaginal apparatus with mesal plate. Character 16: 0 = vaginal apparatus without posterior tubular process; 1 = vaginal apparatus with posterior tubular process. Character 17: 0 = vaginal apparatus without transverse band; 1 = vaginal apparatus with transverse band; 2 = vaginal apparatus transverse band sinuate. Character 18: 0 = vaginal apparatus without lateral plates; 1 = vaginal apparatus with lateral plates. Character 19: 0 = vaginal apparatus rounded or oval; 1 = vaginal apparatus diamond-shaped.

entered as "0" if ancestral and as "1" or "2" if derived, depending on the number of derived states. All characters were equally weighted and considered nonadditive. *Celaenotrichia edwardsi* was designated as the outgroup taxon.

Character analysis and polarization. *Character 1.* Larval pronotum with lacunate areas and with stout apicolateral seta (Holzenthal and Harris, 1992: fig. 1A, B). In separate papers, we suggested that the monobasic Chilean genus *Celaenotrichia* was closely related to *Byrsopteryx* (Harris and Holzenthal, 1993; Harris and Flint, 1993). The larvae of *Celaenotrichia edwardsi* are very similar to known *Byrsopteryx* larvae in overall morphology and ecology, however, the modified pronotum of *Byrsopteryx* is unique to the genus. Larvae of only *B. mirifica* and *B. chaconi* are known. *Celaenotrichia* has an unmodified pronotum, representing the ancestral condition seen in other Hydroptilidae.

Character 2. Forewing with bright white spots made of setae (stripes in *B. rayada*) on a dark fuscous background (Figs. 3, 4, 6, 7). While other hydroptilids have patterns of colored setae and scales on the forewings, we know of no other genus which has such brightly contrasting spots. Furthermore, its bright color pattern coupled with its active diurnal behavior and madicolous habitat render *Byrsopteryx* unique, at least among all other Stactobiini in Costa Rica, where we have many field observations. The structure of the retinaculum and frenulum of *Byrsopteryx* may also be synapomorphic, but we have not investigated these structures in other stactobiines.

Character 3. Forewing venation reduced to only a few longitudinal veins and *Character 4*: forewing with fracture (Fig. 5C). This combination of characters is derived when compared to the more complete pattern of wing venation seen in *Celaenotrichia.* However, other stactobiine genera have varying degrees of reduced venation and some have what appear to be fractures or sutures in the forewing (Harris, unpubl. data). The homology of these venational patterns will be presented by Harris and O. S. Flint, Jr., in a review of the Neotropical Stactobiini. The wing venation in *Byrsopteryx* might represent a more generally distributed stactobiine pattern.

Character 5. Tibial spur formula 0, 3, 4 (Fig. 5B). The primitive distribution of tibial spurs in the Trichoptera is 2 on the foretibia, 4 on the middle tibia, and 4 on the hind tibia, giving a spur formula of 2, 4, 4. Spur formula in *Celaenotrichia* is 1, 3, 4 and in *Byrsopteryx,* 0, 3, 4. Losses of tibial spurs occur frequently throughout the Trichoptera and especially so in the Hydroptilidae, thus the possibility of homoplasy with other stactobiine genera is high.

Character 6. Male abdominal segment VII without ventromesal process. The presence of a small spurlike process on sternum VII (or VI or both) is part of the ground plan of the Trichoptera. Its absence is derived, but again, this is a loss that occurs frequently throughout the order. *Celaenotrichia edwardsi* possesses a prominent ventromesal process. Its loss in male *Byrsopteryx* is derived.

Character 7. Male abdominal segment VIII with long thick setae ventrally (Figs. 9A, 10A). This character state, shared by all of the Costa Rican species, is derived. Abdominal setae in *Celaenotrichia* and other *Byrsopteryx* are shorter and more slender.

Character 8. Male abdominal segment VIII with dorsolateral processes (Figs. 9A, 10A). These processes, found in all of the Costa Rican species except *B. gomezi,* are derived. The bladelike condition seen in *B. cuchilla* and *B. esparta* is a further derived condition. These processes are lacking in *Celaenotrichia* and other *Byrsopteryx* species.

Character 9. Male abdominal segment VIII with thick spinelike mesoventral (and ventrolateral) setae (Figs. 9C, 10C). These modified setae are found only in *B. chaconi, B. cuchilla, B. esparta, B. solisi, B. tapanti,* and *B. tica.* They are derived.

Character 10. Male abdominal segment IX with posterolateral appendagelike processes (Figs. 8A, 9A, 12A, 14A, 16A, 17A). This character is variable within the genus and we are uncertain if the structures are even homologous among the species. The character was coded as multistate, depending on whether the processes were bifid, single and sinuate, or single, sinuate, and with a dorsal seta. The bifid condition was coded as primitive since that is the condition in *Celaenotrichia.* We are especially uncertain about the homology of the bifid condition. Within the bifid state, it is difficult to determine if the process is a single basally bifid structure, or if the process is in fact two separate processes, closely associated basally. Other stactobiines, and some *Alisotrichia* species, have processes located dorsolaterally on segment IX. We do not know if these various structures represent homologies or homoplasies. We are certain that these processes in the Costa Rican species are synapomorphic, because they are very similarly shaped, positioned, and each bears a similarly positioned dorsal seta.

Character 11. Male abdominal segment X with lyre-shaped sclerotization (Fig. 9A, B). The details of structure and shape of segment X in the Costa Rican species indicate synapomorphy. Segment X in the outgroup and other species is not modified in such a way, but there are differences in the morphology of this segment among the other species. We have not analyzed the phylogenetic significance of these differences.

Character 12. Male inferior appendages (Fig. 9A, C). Separate, ventrolateral inferior appendages are part of the ground plan of the Trichoptera. None of the modifications in *Byrsopteryx* are "typical" trichopteran inferior appendages. We are not certain that the tubular structures seen in some *Byrsopteryx* are homologous with inferior appendages, but their ventral position on segment IX is consistent with the position of inferior appendages. The tubular structure may represent a highly modified subgenital plate or an altogether new structure. We have seen no intermediate states between the tubular condition and the typical separate condition. *Celaenotrichia* lacks inferior appendages. The absence of interior appendages was considered the plesiomorphic state and the presence of tubular structures the apomorphic state.

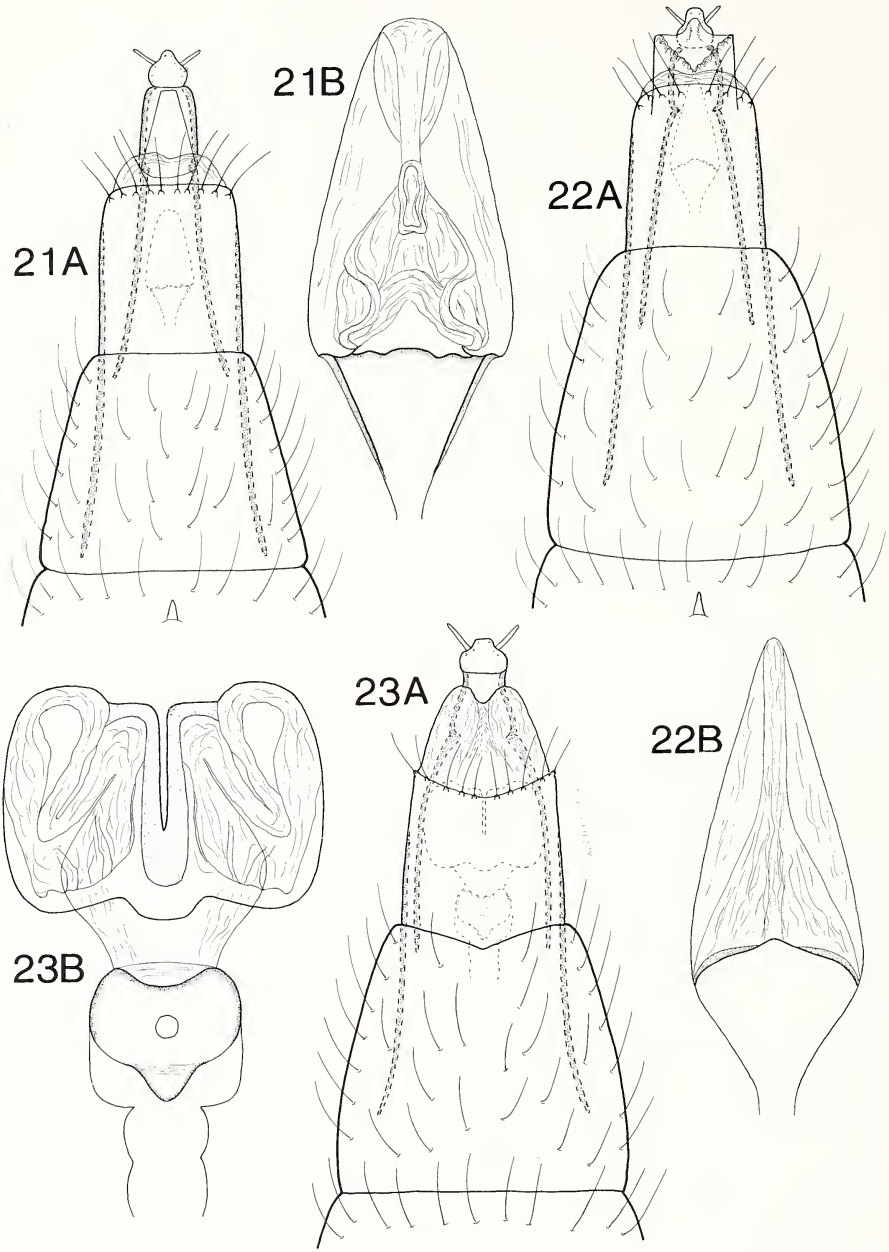
Character 13. Male subgenital plate absent. The subgenital plate is part of the ground plan of the Hydroptilidae. Its absence is considered derived.

Character 14. Female abdominal segment VI without ventromesal process (see discussion under character 6.)

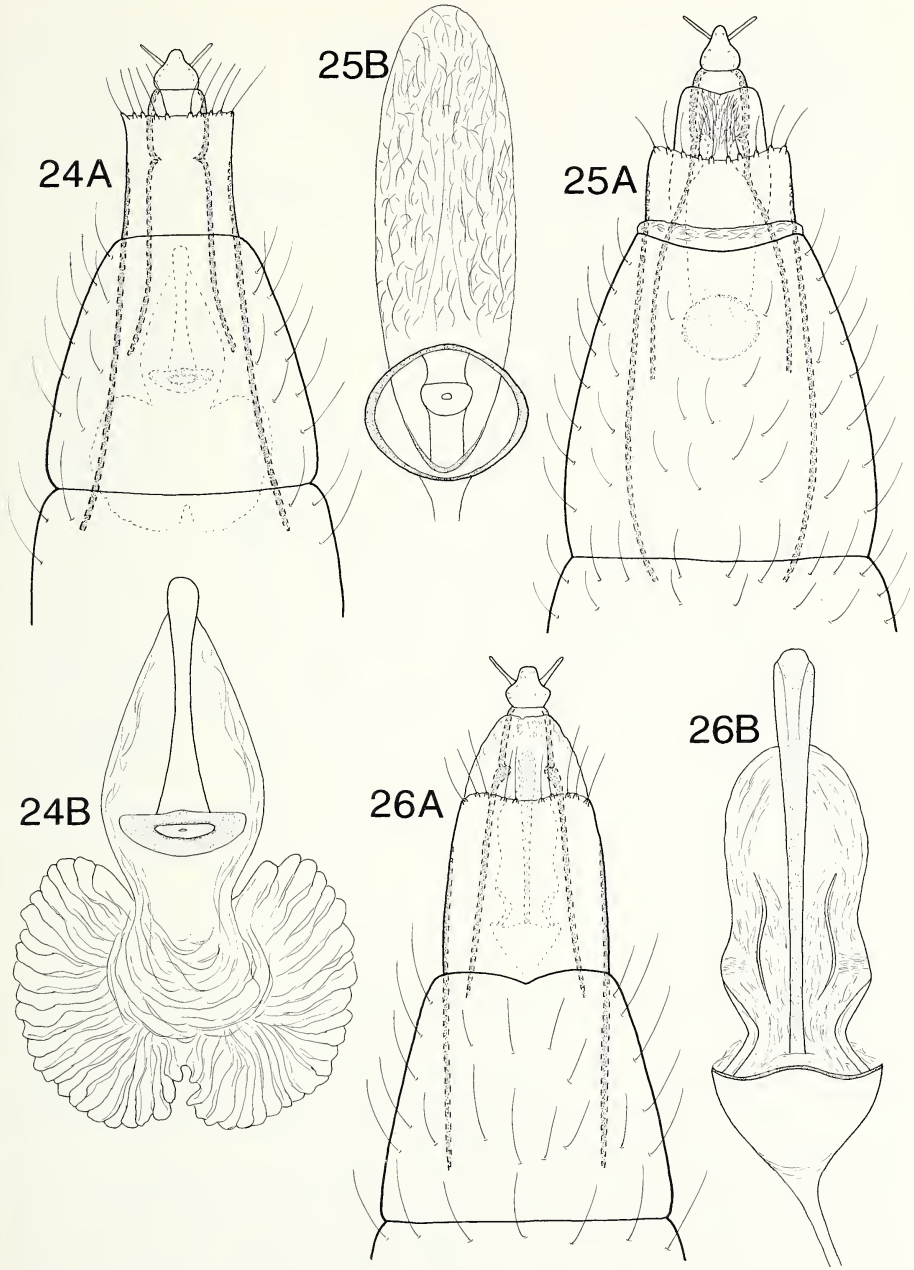
Character 15. Female vaginal apparatus with mesal plate (Figs. 23B, 24B, 25B). This structure is not seen in *Celaenotrichia* and *Alisotrichia* in the Stactobiini nor in *Leucotrichia* in the Leucotrichiini. Its presence in several *Byrsopteryx* species is cautiously considered derived. Homology and morphology of female Hydroptilidae genitalic structures are less well known than those of the male. Our interpretations of this character and those discussed below are highly tentative.

Character 16. Vaginal apparatus with posterior tubular process (Figs. 24B, 26B, 27B, 28B, 29B, 30B). Of all the female characters this one seems to be the strongest synapomorphy. A similar structure is not known in other Stactobiini.

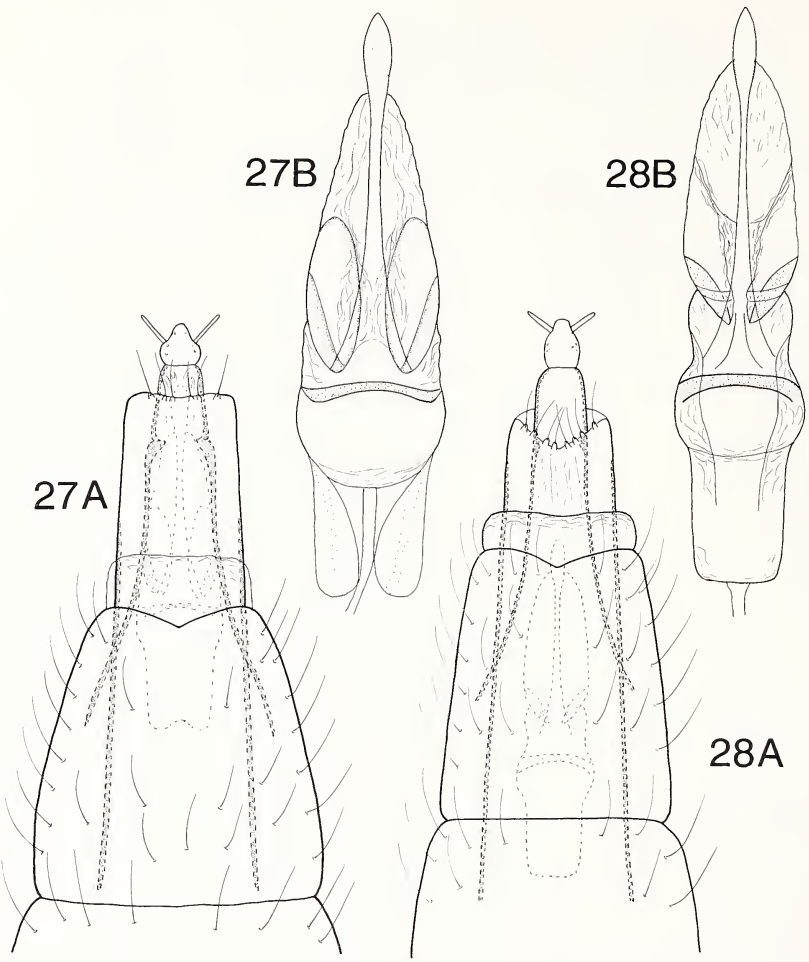
Character 17. Vaginal apparatus with transverse bands (Figs. 27B, 28B), *Character 18:* vaginal apparatus with lateral plates (Figs. 27B, 28B), and *Character 19:* vaginal apparatus diamond-shaped, narrowed anteriorly and posteriorly (Figs. 21B, 22B).



Figs. 21–23. *Byrsopteryx* spp., female genitalia. 21. *B. loja,* n. sp. 22. *B. rayada,* n. sp. 23. *B. mirifica* Flint.



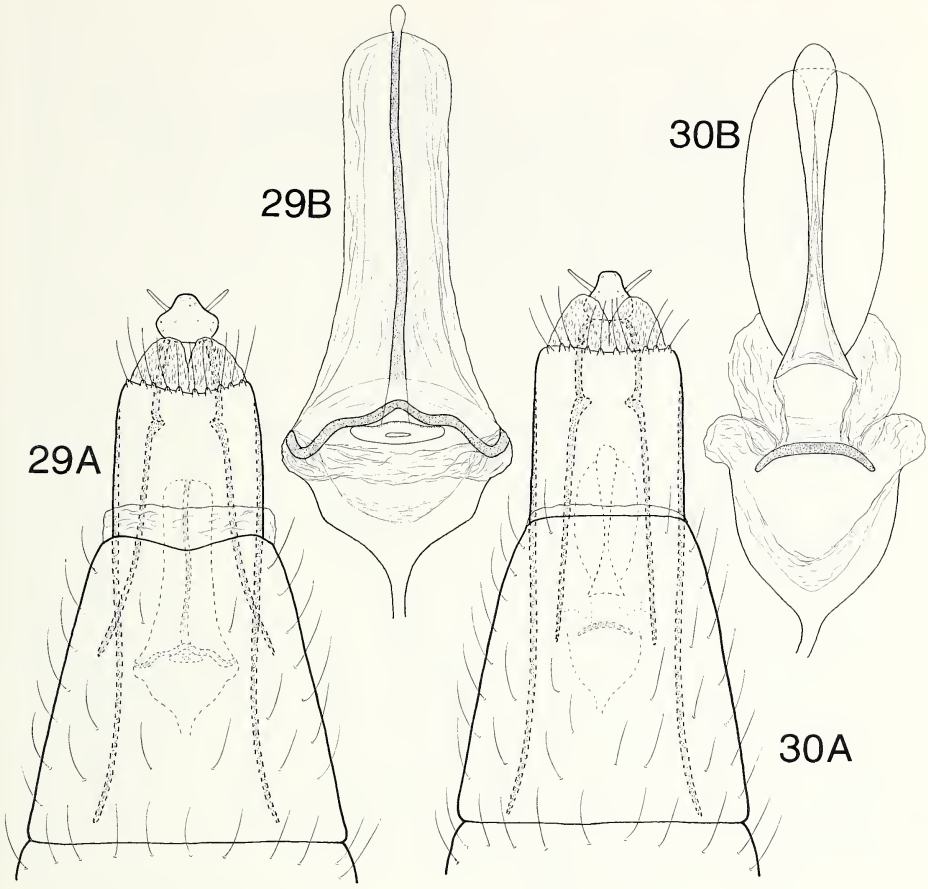
Figs. 24–26. *Byrsopteryx* spp., female genitalia. 24. *B. gomezi,* n. sp. 25. *B. abrelata,* n. sp. 26. *B. chaconi,* n. sp.



Figs. 27, 28. *Byrsopteryx* spp., female genitalia. 27. *B. cuchilla,* n. sp. 28. *B. solisi,* n. sp.

The absence of these bands and plates, i.e., a more simple, fully membranous vaginal apparatus and a more oval or rounded vaginal apparatus, is considered the ancestral condition. The sinuate transverse band of the vaginal apparatus seen in *B. chaconi* and *B. tapanti* is a further derived condition.

Results and discussion. Six equally parsimonious trees were found using PAUP's BRANCH and BOUND tree searching routine with the COLLAPSE option in effect. It took 0.87 seconds to complete the search. Each tree had a length of 25 steps (minimum = 22, maximum = 73), consistency index of 0.880, and retention index of 0.941. Other indices are given in Figure 31. Identical character distributions were obtained under both ACCTRAN and DELTRAN optimizations. The position of only one terminal taxon, *B. espinhosa,* changed among the six trees. Excluding this species from the analysis resulted in a single most parsimonious resolution. Strict,



Figs. 29, 30. *Byrsopteryx* spp., female genitalia. 29. *B. tapanti,* n. sp. 30. *B. tica,* n. sp.

semistrict, Adams, and 50% majority rule consensus trees of the 6 most parsimonious trees had the following tree lengths and C.I.'s respectively: 29, 0.759; 27, 0.815; 25, 0.880; and 25, 0.880. Adams and 50% majority rule consensus trees had identical topologies, equal to one of the most parsimonious trees, and the latter was chosen as the solution tree (Fig. 31). Characters 13, 15, and 17 exhibited homoplasy on the tree. All characters are distributed on the tree as illustrated in Figure 31. Because of our limited information about the fundamental nature of structures in *Byrsopteryx* we chose not to manipulate the data set by weighting or ordering characters.

Our hypothesis of the phylogeny of the species of *Byrsopteryx* is presented in Figure 31. Characters 1–6 support the hypothesis that *Byrsopteryx* is monophyletic. Within the tree, a basal trichotomy exists between *B. espinhosa, B. loja* + *B. rayada,* and a clade of all other species. Character 19 (vaginal apparatus diamond-shaped) indicates a sister group relationship between *B. rayada* and *B. loja.* Characters 14 (females without ventromesal process) and 15 (vaginal apparatus with mesal plate) support

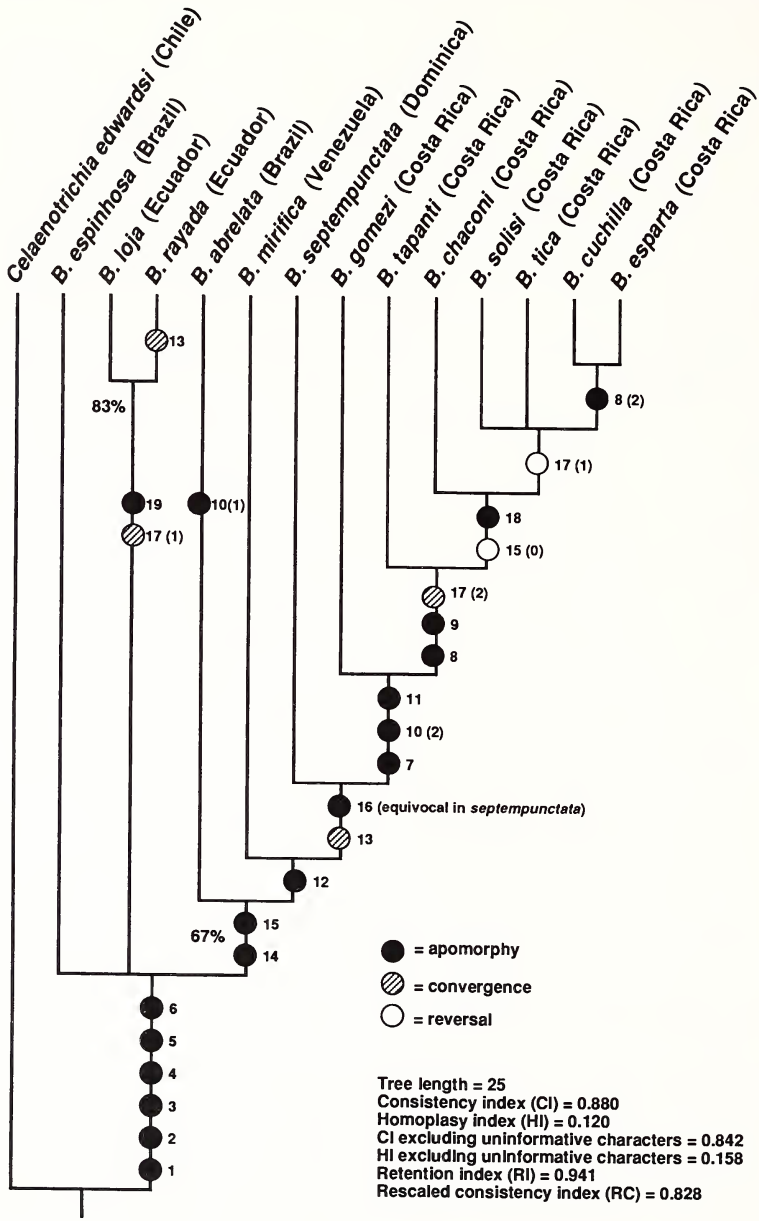


Fig. 31. Phylogeny of the species of *Byrsopteryx* based on 50% majority rule consensus tree of 6 equally parsimonious trees. Percentages at nodes refer to percent of the 6 parsimonious trees containing that particular clade (all clades 100% unless otherwise indicated). Numbers to the right of symbols refer to characters and their states as presented in Table 1.

monophyly of all the species, except *B. espinhosa, B. loja,* and *B. rayada,* although the latter character is lost in all but two of the Costa Rican species. Character 12 (inferior appendages fused, tubular) supports monophyly for *B. mirifica, B. septempunctata,* and a clade containing all the Costa Rican species. Character 16 (vaginal apparatus with posterior tubular process) supports monophyly for *B. septempunctata* and the seven Costa Rican species, although the character is equivocal in *B. septempunctata* since the females of that species are unknown. Absence of the subgenital plate (Character 13) occurs in *B. septempunctata* + Costa Rican clade and its loss appears as a convergence in *B. rayada.* All of the Costa Rican species form a very homogeneous clade defined by character 7 (segment VIII with long thick setae ventrally) and character 11 (segment X with lyre-shaped sclerotization). State 2 of character 10 (segment IX posterolateral appendagelike process single, sinuate, and with dorsal seta) is also synapomorphic for the Costa Rican clade. State 1 of character 10 occurs as an autapomorphy in *B. abrelata.* Within the Costa Rican species all but *B. gomezi* share character 8 (segment VIII with dorsolateral processes) and character 9 (segment VIII with thick spinelike mesoventral setae). Character 17 (vaginal apparatus with sinuate transverse bands) is, in its most derived condition (state 2), shared by two of the Costa Rican species, but is considered to revert to state 1 in the remaining four Costa Rican species (Fig. 31). The latter character state appears as an evolutionary convergence in *B. loja* and *B. rayada.* Character 18 (vaginal apparatus with lateral plates) supports monophyly of five of the Costa Rican species. State 2 of character 8 (segment VIII dorsolateral processes bladelike) indicates a sister-group relationship between *B. cuchilla* and *B. esparta.*

This first assessment of the phylogenetic relationships of the species of *Byrsopteryx* should be considered very tentative. We have questions about the homology of many structures and our decisions on character polarity are open to reinterpretation. We are more certain, however, that *Byrsopteryx* is a monophyletic genus, that it belongs in the Stactobiini, and that within it the seven Costa Rican species form a well defined clade. The discovery of additional species, especially from South America, and the female of *B. espinhosa* will aid future analyses.

The Neotropical Hydroptilidae are a *terra incognita* in terms of both descriptive taxomony and phylogenetics (Flint, 1992). While many hundreds of species have been described, hundreds more await discovery and description. Each new discovery provides information that has changed and will continue to change our views about the phylogenetic relationships within this most interesting family.

KEY TO MALE *BYRSOPTERYX* SPECIES

1 Inferior appendages fused into an elongate, narrow tube (Figs. 9A, C, 13A, C, 17A, C); lateral and ventral margins of segment VIII with thickened elongate setae (Figs. 9, 10, 11, 19, 20) 2

– Inferior appendages absent (Figs. 8A, 14A, 16A) or, if fused, not into an elongate, narrow tube (Fig. 15A, C); margins of segment VIII without such setae 9

2 Abdominal segment VIII with dorsolateral process (Figs. 9, 10, 11 18); with stout spinelike setae ventrolaterally and/or mesoventrally on segment VIII (Figs. 9C, 10C, 18C, 19C) 3

– Abdominal segment VIII without dorsolateral process; lacking stout spinelike setae on segment VIII (Figs. 8C, 14C, 16C) 8

3 Dorsolateral process of segment VIII broad, blunt apically (Fig. 18A); four stout, dark, spinelike setae mesoventrally on segment VIII (Fig. 18C); fused inferior appendages short in ventral view (Fig. 18C) ..... *Byrsopteryx solisi*
– Dorsolateral process of segment VIII narrow, acute apically (Figs. 9A, 10A, 11A, 19A, 20A); two stout, dark, spinelike setae mesoventrally on segment VIII (Figs. 9C, 10C, 11C, 19C, 20C); fused inferior appendages elongate in ventral view (Figs. 9C, 10C, 11C, 19C, 20C) 4
4 Dorsolateral process of segment VIII short or elongate, downturned apically (Figs. 9A, 19A, 20A), in ventral view, curving inward distally (Figs. 9C, 19C, 20C); spinelike setae of segment VIII elongate, straight, or divergent (Figs. 9C, 19C, 20C) 5
– Dorsolateral process of segment VIII elongate, straight, knifelike (Figs. 10A, 11A), in ventral view, only slightly curving inward (Figs. 10C, 11C); spinelike setae of segment VIII elongate (Fig. 11C) or short, convergent (Fig. 10C) 7
5 Dorsolateral process of segment VIII short (Fig. 9A), in ventral view abruptly curving inward apically, broadly shouldered basally (Fig. 9C); phallic apparatus lacking thin, lateral spines (9E) ..... *Byrsopteryx chaconi*
– Dorsolateral process of segment VIII elongate (Figs. 19A, 20A), in ventral view gradually curving inward apically, slightly shouldered basally (Figs. 19C, 20C); phallic apparatus with thin, lateral spines (Figs. 19E, 20E) 6
6 Posterior margin of segment VIII with ventrolateral and mesoventral spinelike setae (Fig. 19A), mesoventral pair thin, straight, parallel (Fig. 19C) ..... *Byrsopteryx tapanti*
– Posterior margin of segment VIII with only mesoventral spinelike setae (Fig. 20A), these thick, widely separated basally, convergent subapically, curving abruptly outward apically (Fig. 20C) ..... *Byrsopteryx tica*
7 Spinelike setae of segment VIII elongate (Fig. 11C); apex of phallic apparatus with thin, flat sclerites (Fig. 11D) ..... *Byrsopteryx esparta*
– Spinelike setae of segment VIII short (Fig. 10C); apex of phallic apparatus with pair of large, lanceolate sclerites (Fig. 10D, E) ..... *Byrsopteryx cuchilla*
8 Segment IX with pair of thin lateral processes (Fig. 17A); inferior appendages membranous laterally (Fig. 17C); phallic apparatus with 5–6 elongate, internal spines (Fig. 17D, E) ..... *Byrsopteryx septempunctata*
– Segment IX with single, elongate, sinuate, lateral process (Fig. 13A); inferior appendages not membranous laterally (Fig. 13C); phallic apparatus with very many mesal and apical spines (Fig. 13D, E) ..... *Byrsopteryx gomezi*
9 Segment IX incised posterolaterally (Fig. 8A); dorsolateral process of segment IX entire (Fig. 8A); phallic apparatus with elongate central spine (Fig. 8D) .. *Byrsopteryx abrelata*
– Segment IX entire posterolaterally; dorsolateral process of segment IX with dorsal and ventral or mesal and lateral subprocesses; phallic apparatus with single, elongate central spine or numerous spines 10
10 Dorsal subprocess of segment IX process elongate, acute, in ventral view spatulate; ventral subprocess short, acute, in ventral view wide (Fig. 12A, C); subgenital plate truncate, distinct (Fig. 12A, C); phallic apparatus with numerous subapical spines (Fig. 12D, E) ..... *Byrsopteryx espinhosa*
– Dorsal subprocess of segment IX process not spatulate, ventral subprocess narrow in ventral view; subgenital process narrow or absent; phallic apparatus with single, elongate central spine 11
11 Dorsal and ventral subprocesses of segment IX rounded apically or wide (Fig. 16A), in ventral view, lower subprocesses wide basally, rounded apically (Fig. 16C); subgenital plate distinct (Fig. 16C); forewings with white stripes (Fig. 7) .... *Byrsopteryx rayada*
– Dorsal and ventral subprocesses of segment IX narrow, acute apically (Figs. 14A, 15A), in ventral view, lower subprocess thin over entire length, acute apically (Figs. 14C, 15C); subgenital plate indistinct or reduced; forewings with spots 12

12 Segment X with elongate, thin sclerotized process from venter (Fig. 15A, B); dorsal and ventral subprocesses from segment IX thin (Fig. 15A, C); inferior appendages present, although fused (Fig. 15A, C) ..... *Byrsopteryx mirifica*
– Segment X lacking elongate process from venter (Fig. 14); dorsal subprocess of segment IX wider than ventral subprocess (Fig. 14B); inferior appendages absent ..... *Byrsopteryx loja*

KEY TO FEMALE *BYRSOPTERYX* SPECIES

(females of *esparta, espinhosa,* and *septempunctata* not known)

1 Abdominal segment VI with short ventromesal process (Figs. 21A, 22A) 2
– Abdominal segment VI without ventromesal process 3
2 Forewings with white bands (Fig. 7); segment IX incised ventrally (Fig. 22A); vaginal apparatus without lateral sclerotization anteriorly (Fig. 22B) ..... *Byrsopteryx rayada*
– Forewings without white bands; segment IX with ventral tapered process (Fig. 21A); vaginal apparatus with lateral sclerotization anteriorly (Fig. 21B) ..... *Byrsopteryx loja*
3 Vaginal apparatus with posterior tubular process (Figs. 24B, 26B, 27B, 28B, 29B, 30B) 4
– Vaginal apparatus without posterior tubular process 9
4 Vaginal apparatus without transverse sclerite, but with oblong mesal plate (Fig. 24B); large membranous lobes anteriorly (Fig. 24B) ..... *Byrsopteryx gomezi*
– Vaginal apparatus with transverse sclerite anteriorly (Figs. 26B, 27B, 28B, 29B, 30B); without membranous lobes anteriorly 5
5 Vaginal apparatus with very thin transverse band (Fig. 26B); posterior mesal process gradually widening distally; laterally with thin sinuate sclerites ..... *Byrsopteryx chaconi*
– Vaginal apparatus with wider transverse band (Figs. 27B, 28B, 29B, 30B); posterior mesal process narrowing at midlength or uniformly narrow 6
6 Vaginal apparatus with posterior process uniformly narrow and originating from an oblong plate (Fig. 29B); transverse band sinuate ..... *Byrsopteryx tapanti*
– Vaginal apparatus with posterior process narrowing at midlength and not originating from an oblong plate (Figs. 25B, 26B, 30B); transverse band curved, but not sinuate ... 7
7 Vaginal apparatus with short oblong lateral plates (Figs. 27B, 28B); transverse band extending from side to side 8
– Vaginal apparatus with long oblong lateral plates (Fig. 30B); transverse band not extending from side to side ..... *Byrsopteryx tica*
8 Vaginal apparatus oblong lateral plates large (Fig. 27B) ..... *Byrsopteryx cuchilla*
– Vaginal apparatus oblong lateral plates small (Fig. 28B) ..... *Byrsopteryx solisi*
9 Vaginal apparatus with pair of large, posterior membranous lobes (Fig. 23B); without thin circular sclerite anteriorly and with large mesal plate ..... *Byrsopteryx mirifica*
– Vaginal apparatus membranous posteriorly, but without large, posterior membranous lobes; with thin circular sclerite anteriorly and with small mesal plate (Fig. 25B) ..... *Byrsopteryx abrelata*

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